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# ZOOLOGICAL RESULTS

BASED ON MATERIAL COLLECTED IN

NEW BRITAIN, NEW GUINEA, LOYALTY ISLANDS

AND ELSEWHERE.

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DURING THE YEARS 1895, 1896 AND 1897,

BY

ARTHUR WILLEY, D.Sc. Lond., Hon. M.A. Cantab., F.R.S. DIRECTOR OF THE COLOMBO MUSEUM, CEYLON.

PARTS I-VI.

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#### ERRATA.

- 1. "Blanche River" where it occurs should read "Blanche Bay."
- 2. In the article by the late Mr Bedford on Holothurians the word "topotype" was wrongly employed at my instigation. It should read "local variety."

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#### PREFATORY NOTE.

THE present issue is the first of a series of five or six similar parts which will be devoted to an account of material collected during my recent expedition to the Pacific in search of the eggs of the Pearly Nautilus. The research was rendered possible by my appointment in 1894 to the Balfour Studentship of the University of Cambridge and by substantial grants from the Royal Society. Perhaps the character rather than the quantity of the material which from first to last came into my hands justifies this method of publication. The general collections which I made have no claim to completeness since they were not part of my special object; but new facts relating to such forms as Nautilus, Peripatus, Amphioxus, Ctenoplana, Balanoglossus, etc., cannot fail to possess a peculiar interest.

Some of these facts have been already recorded in the pages of the Quarterly Journal of Microscopical Science, and it is proposed to incorporate them anew in the present work.

It is impossible to deny that the undertaking was an anxious and an arduous one, and it is on that account that I am the more deeply sensible of the interest manifested in, and the stimulus imparted to my efforts by Prof. Alfred Newton, Mr Adam Sedgwick and Prof. E. Ray Lankester.

On two successive occasions my tenure of the Balfour Studentship has been extended for a year beyond the allotted triennium.

It is my earnest hope that the work now in course of publication will be regarded by the Board of Managers of the Balfour Studentship and by the Government Grant Committee of the Royal Society as an adequate proof of my endeavour to fulfil the commission with which I was entrusted and that it will be acceptable to my zoological confrères.

My thanks are due to those zoologists who are co-operating in the production of this work. Special acknowledgment of services rendered must be made to my friend Mr A. E. Shipley who has undertaken the essential but ungrateful task of reading the proofs.

In due course it is intended that a general introduction comprising an account of my successive voyages shall be published as part of this series and I shall then have further occasion to state my indebtedness to Dr Anton Dohrn, Mr Richard Parkinson of New Britain, Prof. W. A. Haswell, and others, who have favoured me with their valuable assistance from time to time.

A. W.

CHRIST'S COLLEGE, CAMBRIDGE.

Aug. 4, 1898.

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# THE ANATOMY AND DEVELOPMENT OF PERIPATUS NOVAE-BRITANNIAE.

BY ARTHUR WILLEY, D.Sc. LOND., HON. M.A. CANTAB.

With Plates I—IV.

The only previous notice of the occurrence of Peripatus in any of the islands of the Indo-Pacific region is that of a species recorded from Sumatra in 1886 by Dr R. Horst (8)<sup>1</sup>, and subsequently named P. sumatranus by Sedgwick (19). One specimen only was found in the Museum at Leyden in a bottle containing insects said to have come from East Sumatra. Its general characters (e.g. number of spinous pads on legs, position of generative orifice, and shape of primary papillae) were those which are common to all the Neotropical species of Peripatus, New Britain is geographically an intermediate locality between Sumatra and the Neotropical region, but the Peripatus which occurs there does not possess a single external structural feature of importance (apart from sexual dimorphism) in common with the Neotropical species; although by a singular coincidence the female has the same number of claw-bearing legs-24 pairsas the alleged Sumatran species. Under these circumstances, the evidence that the latter was actually found in Sumatra, which Sedgwick regarded as inconclusive, must appear more than ever worthy of suspicion. Nevertheless, the fact that this unique genus is represented in New Britain by the species which forms the subject of the present paper, makes it very desirable that the islands of the Malay and Melanesian Archipelagos should be carefully watched for their peripatine possibilities. For Peripatus is one of those animals whose presence lends a distinct character to the fauna of any region.

The fact was definitely established by Sedgwick, about ten years ago, that the species of Peripatus hitherto described could be arranged in three groups in accordance with their geographical ranges, namely, Neotropical, Australasian and Ethiopian; those from any one of these regions having certain common features. As I have already pointed out in a preliminary diagnosis (25), the New Britain Peripatus cannot be associated with one of the three groups named above, but forms the type of a fourth group which, in correspondence with the nomenclature adopted by Sedgwick, may be designated Melanesian.

Account of Material. The material at my disposal consisted of thirteen specimens, which I obtained myself from the bush at an elevation of several hundred feet above

<sup>&</sup>lt;sup>1</sup> The numbers in brackets refer to the Bibliography at the end of the Paper.

sea-level, during the months of August and September 1897. The exact locality was in the immediate vicinity of a fresh water source and in the gully in which the stream from the source flowed, in the hills behind the native village of Karavia which lies at the head of Blanche Bay, in the Gazelle Peninsula, New Britain. There was a similar source about half a mile distant where I sought in vain for Peripatus. This is not to be wondered at, since the extremely local or sporadic occurrence of Peripatus is well known. The first specimen, a large female, was found beneath decaying leaves, another was taken from a rotten but still standing stump of a cocoa-nut palm, while the rest were found under stones and about the roots of plants growing on the banks of the stream. The earth here was black, and to the unaided eye the Peripatus appeared also quite black and, as the integument has a dull velvety tone and is not glossy like that of the millipedes, there was some little difficulty in distinguishing them amidst their dark surroundings. They were found singly, and it is fair to conclude that Peripatus is not very abundant in that locality. Those that were obtained seemed to be remarkably sluggish, and though I handled them freely I did not once observe the emission of the tenacious slime from the tips of the oral papillae, which is so characteristic of Peripatus. This was possibly due to the time of the year at which they were taken. Hutton (10) says that the New Zealand Peripatus becomes half-torpid during the winter months and will neither feed nor emit their viscid slime at that time of the year "although procreation still goes on" (Hutton). Similar observations have recently been recorded by Steel (23) in the case of the Peripatus of New South Wales.

Preservation. My material was preserved in 4—5 per cent. formol. I immersed the animals in water until they were fully extended and either drowned or at least quiescent, and then placed them directly in the preservative fluid without opening them. If a living Peripatus be dropped into a dish of water it floats on the surface and when forcibly submerged the whole skin becomes covered with an envelope of air presenting a beautiful silvery sheen. Although I did not make any incision in the specimens to allow for the penetration of the formol, this admirable fluid preserved them so well that they arrived home in almost perfect condition, and I am able to give a fairly complete account, not only of the internal anatomy, but also of the embryonic development. Only the youngest stages were not well preserved owing to the resistance to the penetration of the preserving medium offered by the egg-membrane, which is at first very thick and subsequently attenuates.

Name. It is, rather unfortunately perhaps, necessary to consider the propriety of further providing our species with a name having generic or subgeneric value. Sedgwick, in his monograph on the species and distribution of Peripatus (19), did not deem it advisable to create generic subdivisions within the limits of such a homogeneous group as the Onychophora, but the method of description adopted by him as well as the facts which he brought forward, would seem to leave no other course open. In fact, while tabulating the general (i.e. generic) characters respectively of the South African, the Australasian, and the Neotropical groups of species, Sedgwick refrained from definitely naming them.

This want has accordingly been met by Pocock (16) who subdivided the genus Peripatus into three generic groups which he regarded as "equivalent to, or indeed of considerably greater value than, the genera of other orders." These are

- I. Peripatus s. str., comprising the Neotropical species in which the legs are furnished with 4 spinous pads and the generative aperture lies between the legs of the penultimate pair.
- II. Peripatoides, comprising the Australasian species, with 3 spinous pads on legs and generative aperture between the last pair of legs.
- III. Peripatopsis, comprising the South African species, with 3 spinous pads on legs and generative aperture subterminal, between a pair of rudimentary appendages.

I can find no reason to question the validity of Pocock's names except in so far as he ascribes full generic value to them. For various reasons which it would not be profitable to enumerate I prefer to call them subgenera, and with this reservation I add to the preceding, the following name for systematic use:—

IV. Paraperipatus<sup>1</sup>, comprising the New Britain species, with 3 spinous pads and generative aperture behind the last pair of legs.

The above table of definitions of subgenera has a purely systematic value and does not take into account the remarkable differences in internal anatomy and mode of reproduction. Moreover it might produce the impression that IV differed very slightly from III, whereas in most respects it least resembles the latter.

<sup>1</sup> During the correction of the proofs of this paper, a number of the Comptes Rendus de l'Acad. des Sciences Paris, containing a description by Mons. E. L. Bouvier of a new species of Peripatus from the Gaboon district on the West Coast of Africa, has come to hand.

This species, which Bouvier calls *P. tholloni*, possesses certain external characters which indicate that it stands in an intermediate relation between the South African and the Neotropical species. The generative orifice lies between the legs of the penultimate pair as in the latter, but there are only three spinous pads on the legs as in the former. Bouvier states that there are 24 or 25 pairs of legs; the nephridiopores of the 4th and 5th legs do not lie in the centre of the 3rd spinous pad but proximally outside of it; the jaws are of the same type as those of the Neotropical species. If the subgeneric names, given above, are to be retained, as I think they should be, then a fifth subgenus will have to be created for this new species. Bouvier does not state definitely what view he takes of the matter.

[E. L. Bouvier. Note préliminaire sur la distribution géographique et l'évolution des Péripates. C. R. Acad. des Sc. Paris, T. 126, May 9, 1898, p. 1358.]

In a second note (Nouvelles observations sur les Peripatus. Ibid., May 23, 1898, p. 1524), the same author describes a new species from a single specimen which was captured in a house at Popayan, New Granada (Colombia). The name of the collector is unknown. Bouvier names this species *P. tuberculatus* on account of the presence of characteristic wart-like tubercles on the dorsal surface.

In the position of the generative orifice, and in character of the jaws, it resembles other Neotropical species, but, according to Bouvier, it exhibits the very great peculiarity that the legs, of which there are 37 pairs, are provided with 5 spinous pads (except the last 3 pairs). It is much to be desired that more specimens of this species should be obtained. The feet are provided with four marginal papillae, two anterior and two posterior. The jaws, as described by Bouvier, resemble, though differing somewhat from those described and figured by Camerano for *P. quitensis* Schmarda.

Bouvier does not quote Camerano's paper. (Lorenzo Camerano. Sul Peripatus quitensis Schmarda. Atti Acc. Torino, Vol. 32, 1896—7, p. 395.)

#### GENERAL CHARACTERS

Of the subgenus Paraperipatus.

- 1. The females are larger and more numerous and have a greater number of appendages than the males.
- 2. There are three spinous pads on the legs; and the apertures of the enlarged segmental organs corresponding with the fourth and fifth legs, lie in the centre of the proximal pad of these legs.
- 3. The outer blade of the jaw is simple, without a small accessory tooth at the base of the main tooth.
  - 4. The generative aperture is placed immediately behind the last pair of legs.
- 5. Receptacula seminis are present in the female, but there are no receptacula ovorum.
  - 6. The ova are small and without yolk.
  - 7. Embryos in all stages of development may occur in the uteri of one female.

## DESCRIPTION OF THE SPECIES, PERIPATUS (PARAPERIPATUS) NOVAE-BRITANNIAE.

Colour. The ground-colour of the living animal is black and this is seen, with a lens, to be dotted over with large and small brown or brownish-yellow spots. On the dorsal surface the larger brown spots are arranged segmentally in four rows, namely, one row on each side above the bases of the legs and another row on each side of the median line. The median line is occupied, in preserved specimens, by a prominent narrow black longitudinal tract with segmental intensifications; and in the centre of it is a fine light brownish-tinted or whitish line. The black tract is not so apparent in small specimens, but the median white line is more so. The rest of the black ground-colour developed a bluish tinge after preservation in 5 per cent. formol. To the unaided eye the larger segmental brown spots look like more or less square-shaped areas presenting a block-like appearance, and the intervening space is occupied by the numerous smaller brown spots. The median dorsal white line is continued backwards to the anus where it merges into the brown pigment surrounding the latter.

On the ventral surface there is a median row of brown spots surrounding the modified segmental epidermal areas known as the *ventral organs*. The ventral surface generally is less deeply pigmented than the dorsal surface, but the spinous pads of the legs are dark and the pigmentation is also slightly intensified about the segmental grooves at the bases of the legs.

#### EXTERNAL FEATURES.

I. Sexual differences. Of the thirteen specimens in my collection I find three are males. One of these had escaped my notice at the time that the diagnosis of the

species was published (25). They are to be distinguished externally from the females by their less numerous appendages. To judge from the material at my disposal which, including the older embryos taken from the females, amounted to at least 20 specimens, the rule seems to be for the female to have 24 pairs of claw-bearing appendages and the male 22 pairs. But one of my adult males has 23 pairs of claw-bearing appendages (V).

The females attain larger dimensions than the males, ranging in length from 14.75 mm. (X) to 54.75 mm. (II) and in width of body from about 2 to 5 mm. Two of the males (XII and XIII) were of almost equal size, namely 15 mm. long and 2 mm. wide—the third male (V) was considerably larger, attaining a length of 26 mm. with a width of about 3 mm.

The predominance of the female over the male appears to obtain with all species of Peripatus. In *P. leuckarti* (New South Wales) Mr Steel (23) found that out of 579 specimens collected by him in one season, 390 were female and 189 male or 67 per cent. female and 33 per cent. male; and the females were, on the average, one-third to one-half longer than the males.

For the present, I regard the male of *P. novae-britanniae* which had 23 pairs of legs (No. V) as an exception rather than as a frequent variety, because I have taken advanced embryos from the uterus with their full complement of claw-bearing appendages, viz. 22 pairs (I have four such embryos), while less advanced embryos from the same female were found to have 24 pairs of claw-bearing appendages. Thus in specimen No. II the two embryos which lay nearest to the vagina had 22 pairs of legs; while the two younger embryos following upon the first two, had 24 pairs of legs. I cut sections through one of the former and one of the latter, and as I had expected they turned out to be male and female respectively.

In the Neotropical species of Peripatus the females tend throughout to have a larger number of legs than the males, but the numbers vary considerably within the limits of a given species. Thus in *P. jamaicensis* Grabham and Cockerell, the number of claw-bearing appendages is said to vary from 29 to 43 pairs, so that some of the males would have a greater number of appendages than some of the females. [Pocock (16) and Cockerell, Notes on *Peripatus jamaicensis*, Zool. Ang. 1894, p. 341.]

Sedgwick established the fact that in Peripatus the young are born with the full number of legs, none being added after birth. Indeed in the South African species there seems to be a tendency to reduce rather than add to the appendages, in so far that the rudimentary appendages between which the generative orifice lies, which have been called the *anal papillae*, are stated in Balfour's posthumous memoir (2) to be "most marked in small, and least so in large specimens."

In the position of the generative aperture behind the last pair of legs our species superficially resembles the Cape Peripatus more than any other. In the female the aperture is surrounded by tumid lips. Its position in the male is highly distinctive for the species, being placed at the tip of a relatively long backwardly-directed conical papilla [Fig. 10 a and b]. The last-named structure, i.e. the penial papilla, is the unfailing external sign of the male in P. novae-britanniae.

<sup>&</sup>lt;sup>1</sup> Roman numerals in brackets merely refer to particular specimens.

II. Appendages. i. Antennae. I have made an observation with regard to the antennae which may be worth recording, namely, that the annular spine-bearing ridges increase in number during the life of the animal by the intercalation of new rings between the older rings, so that the number of these rings is not a reliable specific feature. In one individual I counted about 33 rings and in another about 50 [Fig. 6].

ii. Jaws. The character of the jaws and oral papillae is adequately shown in Fig. 5. The outer blade of the jaw is quite simple, while the inner blade is provided with a variable number of minor teeth, generally about 5. In the absence of an accessory denticle at the base of the outer jaw-blade, P. novae-britanniae resembles P. novae-zealandiae as well as certain other Australian species or varieties (Fletcher 5). In other Australian forms, e.g. in the larger Victorian species P. oviparus Dendy and in the New South Wales variety P. leuckarti var. orientalis Fletcher, there is an accessory denticle as in P. capensis and P. edwardsii.

With regard to the inner ramus of the mandible or inner jaw-blade there is no diastema between the first accessory denticle and the remainder of the series, such as occurs in the Neotropical species (Sedgwick 19).

iii. Nephridial apertures. The apertures of the enlarged segmental organs of the 4th and 5th pairs of legs are placed in the centre of the proximal pad of these legs [Fig. 7] and sometimes they divide the pad into two disconnected halves, and sometimes again the two halves remain united by a narrow bridge passing distally from one to the other. The division of the proximal pad of the 4th and 5th legs into two separate halves by the intercalation of the papilliform structure which carries the nephridiopore is characteristic of P. capensis, according to Sedgwick. In P. novaezealandiae Sedgwick showed that the portion of the pad which carries the nephridiopore is continuous distally with the rest of the pad. Finally in P. edwardsii the papilla bearing the nephridiopore of the above segments is quite separate from the 3rd pad and lies between the latter and the 4th pad. Thus in P. novae-britanniae, the relations of the 4th and 5th nephridiopores sometimes approach the condition observed in the Cape species and sometimes that of the Australian species. In Fig. 7, one half of the proximal pad is seen to be independent while the other half is confluent with the pore-bearing papilla. Another most interesting variation, which probably is of frequent occurrence in this species, is the presence of a nephridial aperture in the centre of the proximal pad of the 6th leg in addition to those normally present on the 4th and 5th legs. In no fewer than three individuals—all females—(I, III and VIII) such an aperture occurs on the 6th leg of the left side only (Fig. 11). one individual—a male—(V) a nephridial aperture occurs in the middle of the proximal pad of the 4th, 5th and 6th legs of each side of the body. As far as I was able to observe the segmental organ of the 6th leg was not specially enlarged in those cases where its external aperture was abnormally situated. The occurrence of a distally-placed nephridial aperture on the 6th leg can hardly be regarded as a mere instance of meristic repetition, because it does not involve the absolute number of nephridial apertures but only the number of those which are placed in a certain position. There must be some reason for such a position, and the occasional appearance

here of the aperture of a segmental organ whose usual place is at the base and not near the extremity of the 6th leg, looks very much like atavism. Perhaps the enlarged nephridia corresponding to the 4th and 5th legs are the vestiges of an ancestral form in which all or most or some only of the ordinary nephridia served for the passage of the genital products to the exterior. If there were sufficient grounds for accepting this as a legitimate hypothesis it would afford an explanation of, or at least throw light on, the great contrast there is between the anteriorly-placed genital pores of the Diplopoda and the terminal posterior pores of the Chilopoda.

- iv. Segmental grooves. At the bases of the legs on the ventral surface there is, in the older individuals, a series of not very well-defined grooves at the inner ends of which the segmental organs open to the exterior. They are characterised by a rather deeper pigmentation but by no other special feature. They occur at the bases of the 4th and 5th legs although here the segmental organs do not open into them. These grooves are therefore not so distinctive as are the corresponding structures in P. capensis and in P. edwardsii. In the latter they are separated from the apertures of the nephridia (Gaffron).
- v. Crural glands. There are no white papillae on the ventral side of the legs in the male such as occur in most other species of Peripatus. These papillae, when they occur, bear at their tip the aperture of a crural gland. But crural glands may occur without having their external apertures borne on white papillae. In P. novae-britanniae as in P. novae-zealandiae (Sheldon 22) there are no crural glands in either sex.

Wherever they occur they are found only in the male except in P. capensis where they are said to occur in the female also (Sheldon 22). Without denying their occasional existence in the female P. capensis I may say that I have failed to find them present so far as I have looked for them. They are therefore in any case not always present, and I should doubt, on  $\hat{\alpha}$  priori grounds, if they normally occur in the female. There is a well-developed "fat-body" to be seen in sections through legs of female P. capensis and perhaps this has been confused with a crural gland.

In the male *P. capensis* the crural glands are well-defined structures and, as may be gathered from Balfour (2) and Sheldon (22), they are present in all the legs except those of the first pair. Only the crural glands of the last pair of legs in the male *P. capensis* have their external apertures borne on white papillae and these constitute the unfailing

external sign of the male in this species.

In *P. leuckarti* of Australia, of which Fletcher (5) has clearly established the existence of three distinct varieties, viz., typica, orientalis and occidentalis, white papillae may occur in the male on each leg of the first pair only, or of the last pair only, or of all or only some of the pairs with the exception of the first, or of the first five (Fletcher). Here again, however, Fletcher notes that crural pores may occur in the absence of white papillae.

In *P. edwardsii*, Gaffron (6) and Sedgwick (19) have shown that white papillae occur on certain of the posterior legs of the male, often two such papillae on one leg. Thus Gaffron figures a specimen with two papillae on each of the legs of the six praegenital segments and one each on those of the 7th praegenital segment. The genital

and post-genital segments never have white papillae in this species.

Thus the absence of crural glands and of white papillae on the legs of the male of *P. novae-britanniae* is a feature in which this species resembles *P. novae-zealandiae*.

vi. Feet. The variability of the primary papillae which occur on the feet is another interesting peculiarity of the New Britain Peripatus. In all species except P. sumatranus, there are three papillae in the immediate neighbourhood of the claws on each foot. In the African and Neotropical species one of these papillae occurs on the hinder margin of the foot, and the other two papillae lie close together at the anterior margin of the foot. In the Australasian Peripatus there is a primary papilla at the anterior and posterior margins, while the third papilla has a median dorsal position. In P. sumatranus, as described by Horst, there are only two papillae on the foot at its anterior and posterior margins respectively. Sedgwick (19) states that the condition last described is, if true, unique in his experience of Peripatus<sup>1</sup>.

In the Peripatus of New Britain the foot is duly provided with three papillae, two of which constantly occur in the usual marginal positions, but the third papilla may be median dorsal or it may be slightly excentric, or again it may be approximated to the anterior papilla (Figs. 8 a and b). The variation occurs in the feet of individual specimens. In the greater number of cases, so far as I have observed, the dorsal papilla is not median but sub-median or sub-anterior. Thus in one specimen (X) I found that the dorsal papilla was generally sub-median, but sometimes median. In another (XI) on the right side it was median in 10 feet and not median in 13 (in one foot its position appeared doubtful), while on the left side of the same individual it was median in 6 feet and not median in 18. In this specimen, to take a concrete example, the dorsal papilla of the 16th foot of the right side was markedly excentric (Fig. 8 a), while that of the corresponding foot of the left side was accurately median.

The primary papillae in our species are simple conical structures without a constriction separating the distal spine-bearing portion from the rest of the papilla.

#### INTERNAL ANATOMY.

The several subgenera of Peripatus differ from one another very considerably in the constitution of the reproductive organs. Otherwise the main features of their organisation are fairly uniform although it is probable that a detailed investigation of their finer anatomy would reveal certain contrasts among themselves.

#### SEGMENTAL ORGANS.

It has been mentioned above that when the segmental organ belonging to the segment which carries the 6th pair of legs opens distally by a pore situated in the centre of the 3rd spinous pad, the organ itself is not specially enlarged as are those of the 4th and 5th legs, but resembles a normal nephridium.

Here, as in other species of Peripatus, a typical nephridium consists of four principal portions, viz. (1) an outer dilated vesicle or bladder, (2) a coiled portion recurved upon itself so that (3) the thick-walled funnel lies approximately in the same transverse

<sup>1</sup> The third papilla is not figured by Gaffron in the feet of P. trinidadensis (=edwardsii partim).

plane with the bladder; (4) an inner vesicle whose walls usually appear shrunken in section—this is Sedgwick's end-sac, and is a remnant of the true coelom into which the funnel opens. In a series of sections through a young female (IX) of P. novae-britanniae, Sedgwick's end-sac can be demonstrated with the utmost clearness (see Text-figure 1). It can also be easily seen in sections through a mature female (III). The thin membranous wall of the vesicle passes with characteristic abruptness into the thick glandular wall of the funnel. As I shall have further occasion to point out, there is a similarly sudden transition in the connection between the thin-walled ovarian tubes and the thick-walled oviducts, though this is not so pronounced when seen in section. Both Kennel and Gaffron missed the nephridial end-sac which was discovered by Sedgwick.

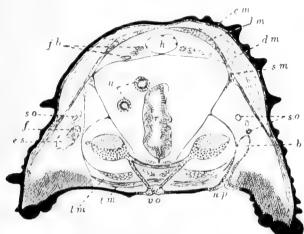


Fig. 1. Semi-diagrammatic transverse section through a young female of P. novae-britanniae.

The segmental organs are represented as seen in a single slightly oblique section. The structures in connection with the nerve-cords are inserted from a combination of several consecutive sections. The ventral nerve-cords are connected with each other by a commissure and with the ventral organ by cellular cords. b. bladder of segmental organ. c.m. circular muscles. d.m. diagonal muscles. e.s. Sedgwick's end-sac. f. funnel. f.b. pericardial cell-groups (so-called fat-bodies). h. heart. l.m. longitudinal muscles. n.p. nephridiopore (a portion of the cuticle is shown entering the ectodermal portion of the excretory tubule). r. rectum. s.m. sagittal muscles. s.o. segmental organ. t.m. transverse muscles. u. uteri. v.o. ventral organ.

There are no segmental organs corresponding to the last pair of legs, either in male or female, in this species; and in the male I have not found a dilated bladder in the nephridia of the 20th and 21st leg-bearing segments. In my sections through these segments the proximal excurrent portion of the nephridium is simply tubular.

#### FEMALE REPRODUCTIVE ORGANS.

On opening a mature female, the first structures to meet the eye are the coils of the uteri and the ramifications of the slime-glands (Fig. 12). The latter extend backwards as far as the ovary, and their smaller branches cohere and intermingle with the convolutions of the uterus. It may be that the slime-glands of Peripatus are comparable to, if not homodynamous with, the cement-glands of Cirripedes, which also interdigitate with the genital organs.

Ovary. The ovary lies primitively dorsally and is attached to the floor of the pericardium approximately in the region of the 21st and 22nd pairs of legs. It appears however from at least one of my dissections either that the floor of the pericardium is capable of being much stretched or that the attachment of the ovary can be drawn out as a ligament, because in the first adult female opened by me, a drawing of which is reproduced in Fig. 12, I had at first some difficulty in finding the ovary, as it was almost completely concealed to the right and below the convexity of the descending portion of the left uterus. By turning the latter aside, the two whitish, closely approximated receptacula seminis came into view. In this example the ovary was coherent with the uterine wall, and a portion of the latter had to be removed and mounted together with the ovary.

The ovary consists of two hollow tubes with thin, folded walls, provided with follicular outgrowths which project into the body-cavity (haemocoel) (Fig. 16). The two cavities end blindly at one end and are separated from one another by a thin septum except near the opposite end, where the cavities unite into a common chamber. The latter communicates by a single aperture with the oviducts which immediately divaricate (Fig. 17). From my preparations it appears that sometimes the oviducts communicate with the ovary at or near its posterior end and sometimes near its anterior end. In Fig. 16 the erect portion of the ovary which enters into connection with the oviducts is obviously posterior. That portion of each oviduct which lies between the ovary and the receptaculum seminis differs in the character of its walls from the rest of the genital duct. The lumen is narrow and the epithelium columnar. In surface view the cells seem to interlace with one another. It requires a special name and I shall call it the infundibulum.

Thus the thick-walled infundibula stand in essentially the same relation to the ovarian chambers as the thick-walled funnel of a nephridium does to its thin-walled end-sac.

The contrast between the infundibula or oviducal tubes and the ovarian tubes which is so striking in P. novae-britanniae does not seem to be exhibited in the

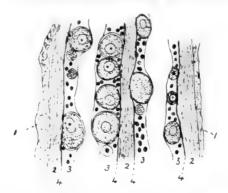


Fig. 2. Horizontal section through the ovarial tubes of P. edwardsii. [After Gaffron.]

- 1. Peritoneum traversed by tracheae.
- 3. Germinal epithelium.

2. Tunica muscularis.

4. Tunica propria.

Neotropical species and has not been remarked upon in the Cape species. In the character of its ovary the Neotropical Peripatus differs fundamentally both from the

New Britain species and from the Cape and Australasian forms. The ovarian tubes in the subgenus Peripatus (see above, p. 3) have thick walls composed, according to Gaffron, of exactly the same layers as the uterine wall, namely, peritoneal investment, tunica muscularis, tunica propria and [germinal] epithelium. The ova mature in situ (Text-figure 2) and make low projections towards the lumen of the ovarian tube, the basal membrane (tunica propria) of the germinal epithelium maintaining its even course below the ova. They may be called "epithelial ova" in contradistinction to the "follicular ova" of the other forms.

In the other three subgenera (see p. 3) the wall of the ovarian tubes is thin and the ova do not retain their epithelial position during maturation, but they cause the wall of the ovary to project in the form of follicles which are attached to the ovary by longer or shorter stalks and hang freely into the central division of the body-cavity (haemocoel) (Fig. 18). In P. novae-britanniae I do not find a tunica muscularis distinct from the peritoneal investment of the ovary, and there is no regular tunica propria. In these respects, the present species resembles P. capensis and P. novae-zealandiae (Sheldon 21).

These facts have their bearing on the interpretation of the morphological character of the ovarian tubes themselves. It is possible that these are not strictly homologous structures throughout the genus Peripatus (see below, section on Receptaculum ovorum).

The ova of our species contain granular protoplasm and are without yolk; when fully formed they measure about '11 mm. in diameter. In point of size they are therefore intermediate between the Neotropical and the Cape species.

Receptacula seminis. The infundibuliform oviducts, which have the shape of ram's horns, lead direct from the ovary to the corresponding receptacula seminis.

Before reaching the receptaculum seminis, each oviduet communicates by a short canal with the uterus. In Fig. 17, this cross-way has the appearance of being a secondary connection. Gaffron (6) has described the origin of the receptaculum seminis by a looping up of the genital duct, the two folds which combined to produce

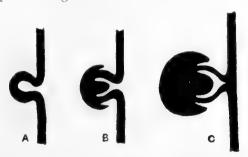


Fig. 3. Diagram to illustrate the mode of formation of a receptaculum seminis with its two ducts. [Simplified after Gaffron.]

In A the oviduct is simply looped.

In B the convex portion of the loop has begun to enlarge and to cause lobe-like projections.

In C the angles of the loop have met and fused.

the loop then fusing together, so that the lumen of the duct becomes continuous past the receptaculum seminis with which it is connected by two ducts (Text-figure 3).

The receptaculum seminis of Peripatus, besides presenting the peculiarity of a double duct, is very remarkable on account of its occurrence in the immediate neighbourhood of the ovary, far removed from the vagina. It occurs in all the subgenera with the exception of the Cape form; and it is always paired. In the young female, 17 mm. long, to which Fig. 17 relates, the receptacula seminis were quite empty. specimens, whether there are few or many embryos in the uteri, there is an abundant supply of spermatozoa in the receptacula seminis; and, as they probably arrive there by way of the vagina, it seems extremely likely that fecundation takes place once only, in other words, that when a female reaches maturity, fecundation takes place, the receptacula seminis are filled with spermatozoa and then ovulation begins. the embryos have begun to pass into the uterus no more fecundation can take place. In the Cape Peripatus, the conditions are widely different. In the absence of receptacula seminis, the spermatozoa penetrate into the ovary itself and fill up its cavity (Moselev 14). Moreover they appear rarely if ever to travel to the ovary by way of the vagina. but they reach the ovary from the outside, being probably injected into the bodycavity through the body-wall by the process described by Whitman as hypodermic injection. In the case of leeches and other forms, this has been satisfactorily observed (Whitman 24). In P. capensis Sedgwick (18) found that the small spermatophores characteristic for this species were deposited upon any part of the body of the female. This observation, combined with Moseley's description, confirmed by Sedgwick and Sheldon, of the ovary filled with spermatozoa some of which projected through the wall of the ovary into the body-cavity, is enough to justify Whitman's suggestion that hypodermic injection of spermatozoa takes place in Peripatus as well as in leeches.

Receptaculum ovorum. In the Neotropical Peripatus there is a thin-walled diverticulum from each oviduct between the ovary and the receptaculum seminis. This sac was mentioned and figured by Grube (7), but its true physiological nature was first ascertained by Kennel (11). This structure only occurs in one known subgenus, Peripatus s. str.

Sedgwick suggested that it was morphologically equivalent to his nephridial endsac. In this case therefore the lumen of the ovary is merely a continuation of the
lumen of the oviduct, and the ovary and its duct are not two structures but one
structure. And this deduction is confirmed by the anatomical facts. The funnel of
the nephridium would thus be represented by the pore leading from the oviduct into
the receptaculum ovorum. This is also borne out by the histology of the parts in
question (Kennel 11, Pt. II) and, as is known, the receptaculum ovorum was described
by Gaffron (6) as the "Ovarialtrichter." In P. novae-britanniae, as we have already
indicated, the appearances are in favour of a distinction being drawn between ovarial
tube and oviduct.

The presence and absence of receptacula ovorum seem to be correlated with the occurrence of what I have called "epithelial ova" and "follicular ova" respectively. In the latter case the stalks of the follicles represent so many secondary ducts discharging into the main ovarial cavity. The latter therefore functions as receptaculum ovorum.

In *P. capensis*, Sedgwick described the segmental origin of the generative organs from the median or generative portions of somites XVI to XX inclusive. The generative ducts arise from the 21st pair of somites (somites of the anal papillae). "The nephridial portion of the twenty-first somite" says Sedgwick (Monograph p. 96) "does not separate from the median or generative portion but remains in connection with the latter and forms the channel by which the generative part of the coelom communicates with the exterior. The generative ducts are therefore modified nephridia, but it is important to notice that the connection between them and the generative tubes is not to be compared with the so-called funnel of the normal nephridia. The latter is merely a special portion of the lateral portion of the somite, and does not seem to be represented in the twenty-first somite."

According to Kennel (11), the sexual organs of *P. edwardsii* (trinidadensis) are nothing else than the metamorphosed segmental organs of the penultimate leg-bearing segment.

In the last-named species therefore the generative organs arise in one segment only. Thus from the beginning to the end the female generative organs of *P. edwardsii* and *P. capensis* appear to differ radically from one another.

In P. capensis the ovarial cavity acts at once as receptaculum ovorum and receptaculum seminis, and is in this respect unique.

In P. novae-britanniae the anatomical relations of the infundibula and ovary involuntarily suggest an exact homology with the funnel and end-sac of a nephridium. I have no observations on the development of these organs.

Uteri. The only parts of the female generative system whose topography is fairly constant, are its two terminal portions, ovary and vagina; what lies between has no regularity whatever in its disposition and it is impossible, from my material, to say whether any particular arrangement is the normal one. In the individual figured in Fig. 12, the outer or vaginal ends of the uteri each contain a pigmented embryo nearly ready for birth. The portion of the uterus which lies posteriorly over the rectum appears from the figure to belong to the right side of the animal. It is really the left uterus and its narrow end passes to the left side and bends under the left nerve-cord to open into the vagina. In another specimen the uteri on being exposed, presented a nearly identical appearance to the one just referred to, but the uterus lying over the rectum in this case turned out to be actually the right uterus and its narrow terminal portion bent down and passed under the right nerve-cord to open into the vagina.

Each uterus on leaving the region of the ovary passes forwards for a varying distance and then bends sharply round upon itself to lead back to the vagina. These two portions of the  $\cap$ -shaped uterus may be referred to as the ascending and descending portions respectively. The distal portion of the uterine tubes, that is, the portion which abuts on the receptacula seminis, is much coiled and the stiff coils will not easily unravel in preserved specimens. In Fig. 13, the ascending right uterus, after emerging from the coil, is seen to pass over and then under the ascending left uterus. Up to this point both uteri are directed towards the ventral side of the body-cavity; but now the ascending right uterus rises to the dorsal side

of the intestine, and retains its dorsal position until its descending portion reaches approximately the point where the intestine passes into the rectum, when it becomes concealed below the left uterus for the rest of its course to the vagina. The ascending left uterus (Figs. 3, 4) has a straight course forwards along the ventral wall of the body-cavity to the right of the intestine until it bends over into the descending portion of the same uterus, the loops of which were deeply imbedded in the wall of the gut. On reaching the point where the intestine passes into the rectum the descending left uterus passes below the alimentary canal from the right side to the left and finally, as we have seen, passes over the rectum with an arcuate bend until it reaches the posterior end of the body, when it passes below the left nerve-cord into the vagina.

In another specimen the entire uterine system lies to the left of the intestine and neither uterus passes below the intestine from one side of the body to the other. In this individual also the distal portions of the ascending uteri embrace and loop round a bend of the right descending uterus (Fig. 15).

There is some evidence to show that, accompanying parturition, either simultaneously or subsequently, a resorption or reconstitution of that section of the uterus from which an embryo has been liberated, takes place. In addition to direct signs of shortening in the terminal (vaginal) region of a uterus, there is the fact that in one female 42 mm. long the uteri extended 15 mm. from the posterior end, while in another which measured 40 mm. in length, the uteri extended 27.5 mm. from the posterior end. Evidence of resorption of the uterus after parturition is also shown by the fact that partially pigmented embryos occurred behind the nearly ripe embryos shown in Fig. 12. Whereas in other cases non-pigmented embryos occur next to the vagina—thus developing in situ. Finally the terminal narrow portion of the uterus lying between the oldest embryo and the vagina, is of varying length. In the Neotropical forms, Kennel has given reason for supposing that a permanent shortening—i.e. resorption—of the uterus is a necessary phenomenon in parturition. An analogous phenomenon has been observed in widely different animals, e.g. Salpa.

# MALE REPRODUCTIVE ORGANS.

It is in the constitution of the male reproductive organs that *P. novae-britanniae* exhibits what is perhaps its most distinguishing anatomical characteristic.

The tubular, more or less hook-shaped, testes debouch into the large ellipsoidal seminal vesicles, as usual at one side of the latter some distance from the anterior tip. The coiled vasa efferentia emerge from the seminal vesicles from a point on the opposite side some distance from the posterior tip. The coiled vas efferens of each side proceeds backwards for a certain distance, when the coils cease and the duct is continued on each side as the straight vas deferens to the extreme posterior region of the body (Fig. 19). Arrived there, each vas deferens passes under the corresponding nerve-cord and then the two meet together in the middle line to form the median ductus ejaculatorius (Fig. 20). Thus the unpaired portion of the male duct is hardly any longer than the vagina. Its actual length would hardly exceed 1.5 mm. including the projecting papilla.

In P. edwardsii according to Gaffron the unpaired portion of the male genital duct attains the remarkable length of 7 centimetres.

In P. capensis the unpaired portion of the duct is much shorter than in P. edwardsii, but is still a fairly long bent tube which does not occupy the median line and is quite asymmetrical (Moseley 14; Balfour 2). According to Moseley's account, which was confirmed by Balfour, the unpaired terminal duct of the Cape species appears to be "a continuation of one of the ducts only, the other duct being cut short and entering "from the side." It may be either the right or the left vas deferens which is directly continued into the terminal duct. Moseley goes on to say that "from the way in which "one duct passes under the nerve-cord [i.e. nerve-cords] and not the other, and from "the curious sharply-turned loop formed by this latter duct on entering its fellow, it "would appear that the original condition had been almost exactly similar to that existing "in the female organs." (Moseley 14, p. 769.)

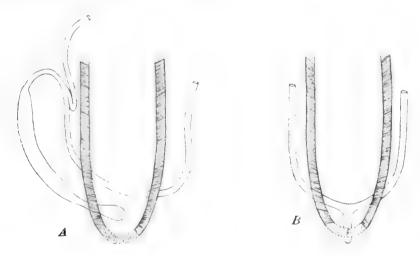


Fig. 4A and B. Terminal portions of the male general ducts of P. capensis (a) and of P. novae-britanniae (b). The shaded structures represent the ventral nerve-cords which pass into each other behind by the suprarectal commissure; A is after Moseley, B is original.

Thus in the symmetrical manner of formation and in the short median course of its ductus ejaculatorius, the male of *P. novae-britanniae* exhibits a distinctly primitive feature as compared with all species hitherto described. This is a matter of some importance in view of the fact that hitherto "no gradation of structure within the genus" (Sedgwick) had been observed.

In *P. novae-zealandiae* according to Miss Sheldon (22) the unpaired portion of the male genital duct is much longer than in *P. capensis* and closely resembles that of *P. edwardsii*. It seems to me that the length of the unpaired portion of the genital duct is in correlation with the production of spermatophores. In *P. capensis* (Sedgwick, Sheldon) the spermatophores are little oval bodies consisting of a thin structureless case filled with spermatozoa.

In P. novae-zealandiae (Sheldon 22) the posterior part of the duct contains

"an enormously long spermatophore which is surrounded by a horny case" and has "precisely the same structure as that described by Gaffron in P. edwardsii."

In P. edwardsii we are informed by Gaffron (6, p. 154) that the spermatophore is a thread-like structure exceeding 4 centimetres in length. This spermatophore has a definite and complicated structure for the details of which Gaffron's excellent Memoir should be consulted.

In P. novae-britanniae the vasa efferentia, vasa deferentia and ductus ejaculatorius contain abundant loose felted spermatozoa, but I have observed no spermatophore.

It must not be supposed that the short median ductus ejaculatorius of the New Britain species is the equivalent of the entire unpaired duct of P. edwardsii and P. novae-zealandiae or even of P. capensis, but it is only equivalent to that portion of the duct in these species which is lined by a chitinous intima and is the true ductus ejaculatorius. In the Cape species the greater part of the terminal duct, upwards of three-fourths, is ductus ejaculatorius and is characterised by its muscular wall and rich supply of tracheae (Moseley). In P. edwardsii the terminal portion of the unpaired duct which, by its muscular walls and chitinous intima, discloses the character of an ejaculatory duct has a length of 2 centimetres (Gaffron).

In *P. novae-britanniae* what there is of an unpaired duct is all ductus ejaculatorius and is alone lined by a chitinous intima. [See Fig. 20 and remarks thereon.]

PYGIDIAL GLANDS. These are a pair of large tubular glands only present in the male and homologous with the accessory glands of the African and Australian species and with the anal glands of the Neotropical species. They resemble the corresponding glands of the other species in their general structure but differ altogether in their method of discharging to the exterior (Figs. 19-22). The glands generally have a dorsal position. The anterior moiety is whitish in the preserved condition while the posterior moiety has a straighter course and a smooth glistening brown-coloured surface with a white axis running up the centre of the tube. The appearance of a white axis is presumably caused by the chitinous intima which lines the ectodermal The whitish, coiled, anterior portion of the gland is the portion of the gland. mesodermal portion. Upon arriving near the posterior end of the body, the two pygidial glands enter a large muscular bulbus, the pygidial bulbus (Figs. 19-22, p. b.). The latter opens to the exterior in the dorsal middle line immediately above and in front of the upper margin of the terminal anal opening (Fig. 19, p. o.). In P. edwardsii the anal glands are so called because they open at each side of the anus as shown by Gaffron. In P. novae-zealandiae, they are described by Miss Sheldon as accessory glands opening near the posterior extremity of the body, the two openings lying outside the nerve-cords and therefore widely separate. In P. leuckarti, Fletcher has described the external openings of the accessory glands as occurring close together between the generative orifice and the anus. Finally in P. capensis they discharge into the terminal portion of the ductus ejaculatorius (Balfour 2).

In *P. novae-britanniae* the muscular coat of the ductus ejaculatorius is not very thick, while the pygidial bulbus occupies a large portion of the mass of the body in that region, and this is particularly the case in late uterine embryos. In *P. capensis* on the other hand the muscular coat of the terminal end of the ductus ejaculatorius is

extremely thick, about as thick, in fact, as the pygidial bulbus of our species; and the two narrow accessory glands enter the muscular mass of the ductus in the Cape species, exactly as the ducts of the pygidial glands enter the bulbus in *P. novae-britanniae*. We have here, therefore, an interesting example of compensating growth.

In *P. novae-britanniae* the external opening of these glands leads into a narrow tube with smooth epithelial lining and chitinous intima. After the median tube has divided and the paired ducts emerge from the bulbus, the lumen soon increases slightly in diameter. At the point where the ectodermal portion of the tube is continued into the mesodermal portion, the lumen becomes suddenly narrowed and the intima ceases. But this constriction is not visible externally because the muscular coat becomes proportionately thicker in this region. The enlarged muscular coat and the reduced lumen continue for a short distance and then the lumen gradually enlarges pari passu with a diminution in the thickness of the tunica muscularis. Finally, the anterior portion of the gland appears in section as a thin-walled tube with very wide lumen, lined by a well-marked smooth epithelium.

The preceding account of the finer anatomy of the pygidial glands (apart from the highly characteristic bulbus) differs from Gaffron's description of the anal glands of *P. edwardsii* chiefly in the fact that in the latter, the external aperture of each gland leads into a wide chamber with folded walls, presenting the same appearance as the rectum itself. So that they are well called anal glands and I think it is advisable to give separate names to structures, even though obviously homologous, when they have such very different anatomical relations.

Kennel (11, Pt. II, p. 70) has shown that in the Neotropical species whose development was studied by him, the anal glands are the modified nephridia of the apodal anal segment. This fact is confirmed by the position of the openings of the corresponding glands in *P. novae-zealandiae* outside the nerve-cords (Sheldon). Kennel further states that a rudiment of these glands is laid down in the female embryos and subsequently undergoes degeneration.

Why do these glands differ so very much in their manner of discharging to the exterior, in one case opening coincidently with the anus, in another opening into the ductus ejaculatorius, in another opening independently with paired apertures between generative pore and anus, and in a fourth case opening by a median dorsal aperture? This is no doubt a difficult question to answer, but the fact that such differences do occur is one of considerable interest. For my part, I am tempted to think that these accessory, anal and pygidial glands of Peripatus are capable of throwing light upon the morphological nature of the Malpighian tubules of Insects and some other Arthropods and of providing an explanation of the fact that these structures are sometimes ectodermal and sometimes entodermal.

¹ Gaffron does not use the word "mesodermal" in describing the anterior portion of the anal glands of *P. edwardsii*, but he described it as "entodermal." I do not know whether he made any mental distinction between entoderm and endoderm—but in any case Kennel objected strongly to the term. If it were not for the risk of falling foul of the germ-layer theory, I should myself prefer the word "entodermal" not as signifying any relation to the technical term "hypoblast" but in simple contrast to "ectodermal." The mesoderm has not the same value as ectoderm and entoderm as has long been realised by many zoologists—but this is a controversial subject. Certainly Gaffron did not mean "hypoblastic" when he used the term "entodermal."

VENTRAL ORGAN AND PAIRED ECTODERMAL ORGANS OF THE ANAL SEGMENT.

Approximately in the same transverse plane with the pygidial orifice, I have observed five shallow epidermal involutions, two dorso-lateral, two ventro-lateral and one median ventral above the ductus ejaculatorius (Fig. 22).

Their symmetrical disposition indicates that they are definite structures and they bear a strong resemblance to the ventral organs. Moreover the median ventral involution is, in fact, the ventral organ of the anal segment, and it occurs also in the female behind the vulva, between the latter and the anus. Of the other involutions I have only observed the ventro-lateral pair in the female where they occur in the same transverse plane with the supra-rectal commissure.

In Fig. 22 the section is taken slightly posterior to the supra-rectal commissure immediately in front of the line of insertion of the free male papilla on to the body-wall, and therefore in the male the ventral organ of the anal segment opens into the angle formed between the penis and the body-wall. In sections through a late male embryo these structures present more the appearance of ectodermal thickenings with slight traces of involution exactly like the ventral organs. The occurrence of paired organs in the anal segment possibly homodynamous with the ventral organ of the same segment is a fact of some interest and importance.

# DEVELOPMENT.

The amount and state of preservation of my material enable me to give an account of the development of *P. novae-britanniae* complete enough to render intelligible the principle according to which it takes place. As I have already mentioned, all stages of development from the segmenting ovum to the fully formed and pigmented embryo are to be found in one adult female.

The first intimation which I received that there was anything remarkable about the embryos of this species was from an examination of the embryo represented on Plate III, Fig. 35. In this figure it is seen that the anterior extremity of the embryo is not coincident with the insertion of the antennae, but there is a long process of the body extending nearly to the tip of the recurved abdomen and covering over the ventral surface of the embryo like a cap, or better still perhaps, like an amnion. It is however not an amnion, but is the remains of a large embryonic vesicle which promotes the nutrition of the embryo and may therefore be called a trophic organ.

For convenience of treatment the development may be divided into twelve stages, which I will at once enumerate.

Stage I. segmentation stages.

" II. formation of blastodermic vesicle.

,, III. embryonic area (including primitive streak) at hinder end of blastodermic vesicle (Fig. 23).

., IV. caudal extension of blastodermic or trophic vesicle, so that the embryonic area becomes removed from posterior end (Fig. 24).

,, V. invagination to form the ventral surface (Fig. 26).

,, VI. forward free growth of primitive streak (Fig. 27).

- Stage VII. oblique U-shaped stage—primitive streak is directed obliquely transverse (Fig. 29).
  - " VIII. involute or O-shaped stage—primitive streak directed backwards (Fig. 30).
  - , IX. spiral or 8-shaped stage (Fig. 33).
  - " X. biflexed or -shaped embryo (Fig. 35).
  - " XI. embryo with simple cephalic flexure or —-shaped embryo.
    - , XII. pigmented embryo nearly ready for birth.

Stage I. As mentioned above, the egg of P. novae-britanniae is small and without yolk, and averages rather more than one-tenth of a millimetre in major diameter. During the first two stages the egg-membrane is remarkably thick ('0075 mm.) and must require special treatment in order to get the contained embryos properly preserved. In my sections through these stages they were all hopelessly collapsed, so that I can give no details as to the process of segmentation. There are indications however that up to a certain point the segmentation proceeds very much as in the Neotropical species as described by Kennel and Sclater, and that it results in a solid morula. But how the inner layer is formed I am quite unable to say. Most likely it arises in situ in the solid morula as in the Mammalian ovum.

Stage II. I have some preparations of embryos in the second of the above stages where an oval cavity with sharply defined contour has appeared in the anterior portion of the embryo, and apparently does not yet extend into the posterior third of the embryo. At this stage the embryo measures 33 mm.

Stage III. In Stage III. the embryo measures about 1 mm. in length. vitelline<sup>1</sup> membrane has become much thinner and consequently this is the first stage of which I obtained adequately preserved representatives, capable of being mounted in toto or of being cut into sections. I had two or three embryos at this stage, one of which is shown in Pl. II, Fig. 16, and another in Pl. III, Fig. 23. The embryonic area proper is confined to a thickened tract at the posterior-ventral side of a large oval The rest of the wall of the vesicle is composed of embryonic ectoderm and endoderm, which however take no immediate part in the formation of the embryo. Physiologically it corresponds exactly with the peripheral epiblast and hypoblast of a Mammalian blastodermic vesicle. As in the latter, it is the ectoderm which is chiefly concerned in the absorption of nutriment for the use of the embryo as evidenced by the vacuolar character of the cells. In view of this remarkable physiological resemblance of this embryonic vesicle to the blastodermic vesicle of a Mammal we may well describe it as a trophoblastic structure, adopting the word trophoblast in the sense in which it has been employed by Hubrecht in relation to the peripheral epiblast of the Mammalian embryo. (Hubrecht 9.)

<sup>&</sup>lt;sup>1</sup> In this species vitelline membrane and egg membrane are used as synonymous terms. In *P. capensis* according to Sedgwick and *P. novae-zealandiae* according to Sheldon there are two membranes, an outer firm membrane and an inner more delicate membrane. The former is often spoken of as the egg-shell or eggmembrane or chorion, and the latter as the vitelline membrane.

Sections through the trophoblastic or trophic vesicle of the present species in front of the posterior ventral embryonic plate show that the wall of the vesicle consists of two layers. The outer layer, the ectoderm, consists of cubical cells of moderate height with vacuolar contents, each containing a large nucleus with usually two "nucleoli." The nuclei of the trophoblastic ectoderm differ from those of the cells forming the embryonic plate, in their staining properties; they take the stain (haematoxylin) less deeply than do the latter. The inner layer, or endoderm, consists of a thin irregular layer of protoplasm applied against the inner surface of the ectoderm and contains scattered globular nuclei which project into the cavity of the vesicle.

The cavity of the vesicle in the early stages is as a rule quite free from foreign bodies of any description, but at a later stage (Stage VIII.) we shall find that it contains many wandering endoderm cells with large nuclei containing a chromatin reticulum with wide meshes—the latter character occurring frequently also in the endodermic epithelial nuclei. These in-wandering cells may be called trophocytes, and compared with the vitellophagous cells in the insect ovum.

The ectoderm of the embryonic plate, except over the primitive streak, consists of a high epithelium with large nuclei densely packed in several tiers. The endoderm here does not differ materially from the peripheral endoderm; sometimes the nuclei are set more closely together than in the latter.

Sections through the primitive streak of an embryo at this stage are given in Pl. IV, Figs. 39—40. Figure 39 passes through the primitive groove. As the series is traced forwards this groove nearly flattens out until, as the anterior portion of the streak is approached, another depression is met with (Fig. 40). This second depression may be called the cranial groove, since in later stages it is bounded by the procephalic lobes.

The interpretation which my preparations lead me to put upon them is that the stomodoeal involution bears a similar relation to the cranial groove to that which the proctodoeal involution bears to the primitive groove.

The extraordinary resemblance of the embryo at this stage to an Insect embryo with short superficial embryonic area on the ventral side of the egg, as occurs in some Orthoptera, as also its likeness to any Insect embryo before the infolding of the embryo (see Korschelt and Heider, 13, p. 774), cannot fail to strike the reader.

When we come to compare the trophic folds of the embryo of *P. novae-britanniae* with the amniotic folds of Insects, this remarkable similarity of the embryos should be borne in mind (see below, p. 32).

Stage IV. Figures 24 and 25 represent portions of two blastodermic vesicles in which the embryonic area no longer has the posterior position seen in the preceding stage. The trophoblastic wall of the vesicle has grown backwards beyond the embryonic plate, so that the latter lies on the ventral side of the vesicle at some distance from the posterior end. In Fig. 24 the embryonic tract has not yet arrived at its definitive location. Fig. 25 is somewhat farther advanced, and it shows well two pits which denote the positions of the primitive and cranial grooves respectively. The ventral surface which commences in the next stage appears as a transverse groove occupying the region between these two grooves.

Figures 46-50, Plate IV, are taken from a series through the embryo represented

in Pl. III, Fig. 25, and will, I hope, suffice to elucidate the structure of the embryo at this stage. As these figures are described as fully as possible in the explanation of the plates at the end of this memoir, I think it will not be necessary to repeat here what is stated there.

Stage V. (Pl. III, Fig. 26). In this stage a transverse groove has formed across the centre of the embryonic area, and pari passu with the appearance of the groove, the ectoderm underlying the groove has become a very thin layer with nuclei arranged in a single row. In the rest of the embryo and in the whole of the embryonic plate of the foregoing stages, the nuclei of the ectoderm are arranged in multiple rows. This transverse groove, which is accompanied by local thinning out or flattening of the ectoderm, is the Anlage of the ventral surface of the animal. It finally separates the cephalic end from the caudal end. The embryo is now to all intents and purposes bent double upon itself, but the doubling up is a passive procedure and is effected in situ by the involution which gives rise to the ventral surface. The flexed embryo is produced, as I have just said, in situ, and a somewhat similar method of development in situ has been described by Miss Sheldon in P. novae-zealandiae where, as is known, the egg is of large size and contains abundant yolk.

Stage VI. (Pl. III, Figs. 27—28). I had one very satisfactory embryo belonging to this stage, and it is faithfully portrayed from the frontal aspect in Figure 27. The total length of the cylindrical blastodermic vesicle, which is now proportionately at its maximum development, was 3.25 mm. It will be noticed how small a tract of this enormous trophoblastic organ is occupied by the embryo proper. It is from the attentive examination of such an embryo as this that one may obtain the best impression of the very singular mode of nutrition of the embryo of *P. novae-britanniae*.

The ventral transverse groove now appears crescentic in shape in surface view. This effect is due to the growth of the primitive streak which becomes raised up from the surface of the vesicle and projects forwards, arching over the ventral surface. As in all other cases where it occurs, the primitive streak is here essentially the growing point of the embryo. It consists of a solid undifferentiated mass of cells which by their remarkable power of proliferation cause the caudal end of the embryo to twist and turn in the manner characteristic for this species. Thus the anterior region of the embryo is practically a punctum fixum, and the contortion of the embryo in a later stage is almost entirely due to the growth which is taking place at the primitive streak. At this stage the free growth of the latter has already commenced but the embryo is still symmetrical, and that is why it is so instructive. It cost me a struggle to cut this unique embryo up into sections, but it had to be done and the result was satisfactory. So well were these embryos preserved in the formal solution which I employed, that mitotic figures are frequently met with in the mesoderm. In surface view the somites of the anterior region were distinctly visible, and the first three pairs of somites can be seen in Fig. 28. From the figure referred to it will be at once evident that a single transverse section may involve several pairs of somites. For at this stage, as in the preceding stage, the transverse diameter of the embryo proper is nearly twice the length of its antero-posterior axis.

Figures 51—57 will sufficiently elucidate the structure of this embryo. Fig. 51 is taken through the centre of the primitive streak which, as already described, now projects in a tongue-like manner over the depressed ventral surface of the embryo. The greatest number of somites which I have met with in a single transverse section was five on each side in sections passing posterior to the primitive streak and tail-swellings, through the region of the backwardly directed cornua of the crescent-shaped embryo.

In consequence of the folding over of the primitive streak, the primitive groove now appears to lie on the reversed side as compared with previous stages (cf. Figs. 39, 48 and 51).

I would further direct special attention to the condition of the stomodoeum in this stage. This is the first appearance of the true stomodoeum, and its lumen is enclosed within the thickness of the ectoderm at the base of the cranial groove on each side of which the praeoral lobes are commencing to project (Fig. 55). This enormously thickened ectoderm is the rudiment of the cerebral ganglia, and only occurs through a few sections. A section or two in front of that shown in Fig. 55, the ectoderm undergoes considerable reduction in thickness, and the blind end of the stomodoeum is cut tangentially (Fig. 56). Thus the stomodoeum precedes the proctodoeum in time of appearance, and this holds good also for *P. novae-zealandiae* (Sheldon 20) and *P. edwardsii* (Kennel 11).

Stage VII. (Plate III, Fig. 29). In this stage the primary symmetry of the embryo is lost owing to the oblique direction into which the caudal end of the embryo becomes bent as a necessary result of its continued growth. The first pair of somites are now present as prominent lobes. They are not free however but attached by their dorsal sides throughout their whole extent to the wall of the trophic organ. This condition will be again met with in the next stage.

Traces of the crescentic form of the embryo as seen in Stage VI. can still be observed in this embryo. The primitive streak is the cause of the contorted shape of the embryo. The free caudal extremity is now no longer directed forwards as it was in the last stage but it is directed to one side and consequently the whole embryo is twisted on to one side. The embryo is now in a state in which transverse sections are of next to no avail. The total length of the embryonic vesicle shown in Fig. 29 was 4.25 mm. In Fig. 29  $\alpha$  another embryo belonging to this stage is shown in which the primitive streak is directed quite transversely. The praeoral lobes and the caudal process are the prominent features of the embryo at this stage.

Stage VIII. (Pl. III, Fig. 30). In this stage the continued flexure of the embryo brought about by the growth of the primitive streak has resulted in the restoration of a certain amount of symmetry in the topographical relations of the various regions. Accordingly sections through an embryo at this stage are instructive.

In addition to the more or less continuous endodermic layer which lines the wall of the trophic cavity, the latter now contains numerous wandering amoeboid cells or trophocytes, which have been mentioned above. These are endoderm cells which have relinquished their epithelial connections and wandered into the cavity of the vesicle. They are present in great numbers in this stage and up to Stage X. All the endoderm cells appear to be potential trophocytes.

In Fig. 30, the free-growing point or caudal extremity of the embryo is directed backwards so that transverse sections will pass accurately through the primitive streak

(Fig. 65). I think Figure 31 speaks for itself. The enormous trophic organ (trophoblastic vesicle) which is such a remarkable characteristic of these embryos, is here clearly seen to be a dorsal structure. The rudiments of the appendages are clearly represented. From the preparations it is evident that the thickened ectoderm which takes part in these rudiments also gives rise to the ventral organs from which the nerve-cords are delaminated. This intimate primary union, in such a form as Peripatus, of the appendicular and the neural folds or thickenings, may be a fact of profound physiological meaning. For, presumably, the forefathers of Peripatus were amongst the earliest terrestrial animals to acquire pedal locomotion. When viewed from a purely physiological stand-point one is inevitably reminded of the lateral line of lower Vertebrates and its possible relation to a more or less hypothetical continuous lateral fin-fold or appendicular ridge.

The complementary functions of locomotion and equilibration combined with the fact of the united origin of nerve-cords and appendages so far as the ectoderm is concerned, may go some way towards explaining or giving a reason for the divarication of the nerve-cords of Peripatus. The old idea held 40 years ago, was, that this indicated a relationship to the Plathelminthes. I think it is safe to say that this view has now a chiefly historical interest.

It might be inferred, from the double fold in the embryo at this stage, that sections through the middle region would involve three distinct portions of the embryo; and such is the case, as a glance at Figures 63—65 will show.

The stomodoeum (Figs. 59—61) is now present as a long tube opening to the exterior at its posterior end at the base of the cephalic lobes and consequently at the base of the cranial groove which lies between the latter. The stomodoeal tube extends at present straight forwards, below the ectoderm of the cranial groove, and ends blindly at its anterior end.

This stage is also characterised by the origin of the segmental organ of the 3rd pair of somites (Fig. 62). It arises, as do all the segmental organs, in the hinder somatic mesodermic wall of the somite. It is a tube opening anteriorly into the somite and ending, at present, blindly at the other end. A vestigial segmental organ in the form of a deep pit in the somatic mesoderm occurs also in the second somite but it is not shut off as a tube from the rest of the somite (Fig. 61). No other segmental organs are present at this stage, and I have not attempted to follow their further development with the limited material at my disposal. If any zoologist should have the opportunity on some future occasion of examining these embryos in the fresh condition, I should recommend him to look for the possible occurrence of cilia in connection with the somatic walls of the somites. The segmental organ of the 3rd somite at this stage looks, in my sections, as if it might be ciliated. The general absence of cilia in the adult Peripatus, except in the male genital ducts and in the ducts of the receptacula seminis in the female where they were discovered by Gaffron whose observation was confirmed by Sedgwick (19), is no doubt connected with the great reduction of the coelom in the adult.

<sup>&</sup>lt;sup>1</sup> I may be permitted to refer to what I have said on this subject in a former publication (Amphioxus and the Ancestry of the Vertebrates, 1894, p. 42).

In this stage the meso-somatic wall of the somite is thicker than the meso-splanchnic wall. In the latter there are often relatively wide intervals between the scattered nuclei whereas they are always compact and often many-layered in the somatic wall. In the first somite, however, the mesodermic layer is uniformly thick, the nuclei occurring throughout in a single row.

Stage IX., Fig. 33. This is the stage at which the embryo is coiled upon itself I have seen other embryos of approximately the same age as this which were not spirally coiled but merely flexed, and it may be stated that every embryo does not necessarily pass through a stage in which it is coiled exactly in this manner (Fig. 33 a). The caudal extremity of the body has now grown to such an extent that it has come to lie in front of the head. The cephalic end of the embryo has maintained its primitive position, and there is, as yet, no cephalic flexure but only caudal and abdominal flexures. A true cephalic flexure is met with for the first time in the next stage. The antennae have now made their appearance as outgrowths from the cephalic lobes, or to speak perhaps more correctly, the cerebral ganglia have become differentiated from the ectodermal thickenings at the bases of the cephalic lobes while the antennary portions of the lobes have increased in length and independence. This is the stage during which the lips which enclose the 2nd pair of appendages—the manducatory appendages—are formed (Fig. 37). The eye-vesicles are also present. The optic groove was present in the preceding stage (Fig. 59).

Rotation of Stomodoeum. The stomodoeum no longer extends straight forwards but is directed dorsalwards. In still later embryos the stomodoeum is seen to project as a stout funnel-like tube backwards and somewhat dorsally from the mouth (cf. Fig. 36). In the present stage it stretches dorsally and somewhat anteriorly from the mouth and is now best seen from the dorsal aspect of the animal. In earlier stages, as we have seen, it was directed straight forwards. This stage of its development is therefore intermediate between its primary forward direction and its secondary definitive backward direction. Thus, in effect, the stomodoeum is rotated through 180°. In the later stages it is best seen from the lateral aspect. A similar rotation, the result of differential growth, has been described by Gaffron in connection with the development of the female generative organs of P. edwardsii. The following is the passage referred to in the second part of Gaffron's work on the anatomy and histology of Peripatus (6, p. 147):—"Bei einem..... Embryo von 1.8 cm. Länge... findet man vor Allem, dass das Ovarium seine Lage um 180° geändert hat, indem es jetzt von seinem Befestigungsort nicht mehr nach hinten, sondern nach vorn gerichtet ist." (See Gaffron, loc. cit. Taf. xxi., Figs. 1 and 2.)

Such instances as these of the ontogenetic transposition of parts are probably of some importance. It is at least a remarkable fact that the stomodoeum of *P. novae-britanniae* occurs at first as a praeoral tube and is later transposed into a post-oral tube. This is not a mere playing with words, because, what is at first the anterior extremity of the stomodoeum becomes, after the transposition has been effected, its posterior extremity.

Stage X. (Pl. III, Figs. 35 and 36). In this stage the relative dimensions of the trophic organ and embryo have undergone a considerable change, and were it not for the remarkable procephalic prolongation of the vesicle which is still present in Figure 35,

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there would hardly be occasion to speak any longer of a trophic organ. In short the vesicular character of the latter is now disappearing and the trophic cavity is becoming nothing else than the definitive gastral cavity. Figure 36, which also belongs essentially to this stage, shows a variation in the flexure of the embryo, the head not being bent under and pointing (when lying in the uterus) accurately in the direction of the vagina. Moreover in this figure the trophic vesicle is more restricted than in Fig. 35, and there is only a small procephalic prolongation of it which does not arch over the ventral surface of the embryo. Possibly this embryo would never have gone through a stage with cephalic flexure. There seems to be some latitude in the amount of flexure which it is necessary for an embryo to undergo. Shortly after this stage the trophoblastic vesicle becomes quite absorbed into the composition of the embryo.

Stages XI and XII. These stages differ from one another chiefly in the amount of pigment which has been deposited in the integument and it will be convenient to treat them together. The full complement of legs is present and it is therefore possible to determine infallibly male and female embryos. They do not differ materially in size—their length, which represents approximately the length of the young at birth, averages about 15 mm.—but the male embryo has 22 pairs of ambulatory appendages and the female has 24 pairs. I have examined sections through such embryos for the purpose of confirming the determination of sex and found the conclusion well grounded. The section of an ovary, shown in Fig. 18, is from a female embryo belonging to Stage XI. In the male the sexual organs are also well differentiated and the pygidial bulbus appears even more pronounced relatively than in a mature male.

In the two oldest embryos which I obtained (belonging therefore to Stage XII) the antennae and entire dorsal surface were darkly pigmented but the ventral surface was on the whole unpigmented. The head and neck were bent under the abdomen, the 2nd leg lying in the bend. The antennae in one were stretched out along the abdomen and in the other were bent back under the head. These embryos were taken from one female and were lying in the terminal portions of the uteri next to the vagina. I have never found a darkly pigmented embryo in any other portion of the uterus than this, but I have found an unpigmented embryo in this position.

From the same female from which these embryos were taken, the embryos following them belonged, in accordance with the successional mode of development followed by this species, to Stage XI. The antennae were pigmented as in Stage XII but the dorsal surface was only very faintly pigmented, the general colour effect being whitish with faint greenish tinge.

Although in all extensive collections of Peripatus which have been made, as well as in my own, the males are much less numerous than the females, yet, singular to say, the two oldest embryos in each of the two females which I opened first, were all four of them males, and three of the embryos immediately following upon these respectively were females. The fourth was probably a female but I could not count the number of its appendages. This order may be a mere coincidence but at first sight it suggests a periodicity in the production of males and females and any future observer of this species should pay attention to this matter.

ORIENTATION OF THE EMBRYO. The embryos without exception, from the youngest in which the anterior and posterior poles are discernible, to the oldest, are placed in one direction. That is to say, the polarity of the embryos is constant. The anterior end of the embryo is invariably directed towards the vaginal end of the uterus. Thus, when an embryo is lying in the ascending portion of the uterus, its anterior end will point towards the head of the mother, and when it comes to lie in the descending portion of the uterus it will head towards the posterior end of the mother. Peripatus offers an interesting example of the comparatively late appearance of bilateral symmetry. There can be no question of bilateral symmetry throughout the segmentation stages. In P. novae-britanniae it probably appears coincidently with the formation of the trophic cavity.

# TRANSFORMATION OF THE TROPHIC CAVITY OF THE EMBRYO INTO THE GASTRAL CAVITY OF THE ADULT.

Although I have correctly stated above that the trophic cavity of the embryo becomes the gastral cavity of the adult, the transformation of the one into the other is not such a simple matter as might be supposed. The embryonic endoderm which was largely used up in the production of the trophocytes in Stage VIII has to be reconstituted, and this reconstitution is accompanied by some remarkable phenomena, chief among which is the appearance of very numerous eosinophile globules in the wall of the gut. I cannot attempt to give full details as to the processes involved in the reconstitution of the wall of the gut, but can only indicate the broad outlines.

The first indication of change in the endodermic lining of the trophic cavity that I have observed, appears in Stage X. Here the endoderm with its scattered nuclei is seen to separate from the ectoderm leaving a space between the two layers. The space thus left between ectoderm and endoderm is the commencement of the definitive body-cavity or haemocoel and in it are to be observed wandering mesoderm cells, There is a fairly continuous somatic layer of mesoderm but no splanchnic layer at The latter appears to be represented at first merely by the wandering mesoderm cells. The somatic layer probably grew out from the somites between the ectoderm and endoderm before the separation of the latter to form a space. I have clear indications of this in my preparations. This observation coupled with that of Sedgwick's nephridial end-sac (see p. 9) may I think be regarded as an indirect corroboration of Sedgwick's account of the history of the somites in P. capensis. cells of the endoderm have secreted a fine basal membrane, the membrana propria of the gut, to which they appear more or less loosely attached and from which they project boldly into the gastral cavity. Indications are not wanting that the wandering trophocytes apply themselves to this membrane and take part in the formation of the gastral epithelium.

In sections through an embryo belonging to my Stage XI, which is considerably farther advanced than the preceding stage, the dimensions of the trophic or gastral cavity are much more reduced, there is a wide body-cavity, and the endoderm cells which in the preceding stage were described as projecting into the gastral cavity have now attained a great height ('09 mm.) and moreover have secreted another membrane—a cuticular membrane—at their free ends. There are no definite cell outlines but

between the basal membrane and the cuticular membrane are stretched irregular strands of protoplasm up the centre of which may often be traced a fine supporting axis which perhaps represents a cell-membrane. The strands of protoplasm are beset with innumerable eosinophile globules of varying sizes. The supporting axes mentioned



Fig. 5. Portion of the endoderm of P. novae-britanniae at stage x.

The coarsely granular endoderm-cells or trophocytes lie upon the membrana propria projecting freely into the trophic cavity. The cells are often separated by wide intervals.

above, which stretch from membrane to membrane, obviously serve the purpose of holding the granules in position and, on the other hand, the cuticular membrane which is a temporary structure and not always if ever present in the adult, serves the purpose of providing a point d'appui for the strands of protoplasm with their globules. The nuclei lie near the base of this thickened epithelium.



Fig. 6. Portion of the wall of the mid-gut of P. novae-britanniae at stage XI.

The endoderm has become a thickened compact layer containing numerous eosinophile globules. The cuticle at the inner surface of the endoderm has become (artificially) separated at this point from the cells which secreted it, this portion of the section having been selected for representation in order to show the membrane as a distinct cuticular product. The protoplasmic matrix of the globules is not shown in the figure.

In Stage XII this remarkable epithelium (which has meanwhile still further increased in thickness) with its contained eosinophile globules is, in my preparations, in process of undergoing complete disintegration. The cuticle is ruptured locally and the globules are passing singly and en masse into the gastral cavity presumably preparatory to their resorption. In other words, the wall of the gastral cavity is undergoing a histolytic change and the scene presented while it is doing this, is one of the utmost disorder. In this stage the globules average larger and are somewhat less numerous than in the preceding stage.

These globules are clearly the product of the metabolism of the endoderm cells which have converted the nutrient matter derived from the maternal fluids into

<sup>1</sup> This is true of the posterior region of the particular embryo referred to. In the anterior region the changes are far less advanced although there are indications of their approach.

yolk-like bodies, possibly as a reserve food-stuff to tide the newly-born young over the first few days of its independent existence.

This late appearance of yolk-like globules, if they are not actually identical with true yolk, seems to me to be a fact of some interest.

In *P. capensis*, Balfour (2) described the gastral epithelium of the adult as consisting of much elongated fibre-like cells attaining a maximum height of nearly 5 mm. He says "the cells are mainly filled with an immense number of highly refracting spherules, probably secretory globules, but held by Grube, from the fact of their dissolving in ether, to be fat<sup>1</sup>." Balfour goes on to say, "The epithelial cells are raised into numerous blunt processes projecting into the lumen of the stomach." But in his Figure 20, Plate XVIII, the gastral epithelium is represented with a smooth inner surface.

By globules I refer to the bodies described above in late embryos of P. novae-britanniae which vary much in size between a minimum and a maximum.

By spherules are intended minute round bodies of generally uniform size.

I have seen Balfour's spherules in *P. capensis* and also in *post partum* young of *P. leuckarti* and *P. novae-britanniae*. They react towards staining media differently from my globules. They do not take the eosin nearly so readily as do the latter.

In his well-known work on the histology of Peripatus, Gaffron is absolutely reticent about the histology of the gut. Was it because he could not understand the appearances presented?

Unfortunately I cannot give any decisive account of what does actually take place. This could only be attempted with an abundance of fresh material at one's disposal. But enough may be said to show that the subject is one of singular interest.

From what I have seen I am led to the conclusion that Balfour's account of the gastral epithelium of Peripatus is only true of one phase—a periodically recurring phase—in the life-history of Peripatus. There are long periods during which Peripatus

<sup>&</sup>lt;sup>1</sup> The yolk-like globules in late embryos of our species were not dissolved after 4 hours' treatment with chloroform.

takes no food. During such periods life must be sustained by the absorption of reserve nutrient matter, and it would probably be found, if the subject were investigated, that the gastral epithelium undergoes profound changes and differs immensely during a period of feeding from its condition during a period of rest.

P. novae-zealandiae does not feed during the winter months (Hutton). In the colder months, P. leuckarti becomes sluggish and remains for considerable periods without eating (Steel). With regard to P. capensis, Moseley (14, p. 762) says "It is very possible that the animals feed very little or not at all during the breeding-season, but rest, as does Julus according to Newport, at the time of the production of the eggs."

It is further possible that the nutrition of the free-living Peripatus is affected during the moulting periods. Hutton's observation of the occurrence of the so-called reserve teeth below those in actual use rendered it probable that moulting did take place in Peripatus. This has now been finally observed by Steel (23). Steel obtained several perfect casts from both young and adult individuals. He however did not observe how often this ecdysis recurs.

In my sections through a young post partum female of P. novae-britanniae, there is no regular gastral epithelium at all, but nuclei occur in numbers irregularly distributed in the gastral cavity in the midst of a mass of foreign, presumably ingested material. I found a similar condition in a young male. From these observations I am led to the following conclusion, which is of value only as a working hypothesis. During certain periods the gastral epithelium is a regular columnar epithelium as described by Balfour, and its cells contain abundant spherules of reserve nutrient matter. At certain other periods, perhaps periods of rest, the gastral epithelium undergoes histolysis, and the endoderm performs its function of digestion by a process allied to phagocytosis, its cells having exactly the properties of the trophocytes which I have described above in certain stages of the development of P. novae-britanniae.

I have little doubt that in discharging its digestive function Peripatus is quite as original as it is in every other respect<sup>1</sup>.

The young female referred to above, in which I observed this extraordinary "wandering endoderm," was the specimen in which the nephridial end-sacs were so capitally preserved.

With regard to the globules described above in late embryos of *P. novae-britanniae*, the smallest of them are much smaller than Balfour's spherules but, as already stated, they behave differently towards staining reagents. The largest globules in Stage XI measure '0125 mm. in diameter, in Stage XII nearly '02 mm. Possibly the larger ones are sometimes produced by coalescence of smaller ones, and this would account for their larger size in Stage XII.

Besides differing in chemical properties, the globules differ from the spherules in their source, in that while the latter owe their origin ultimately to foreign ingested matter, the former are derived from the maternal organism.

Finally, with regard to the histolysis which my sections show in Stage XII, it is to be noted that it takes place pari passu with the opening of the proctodoeum into the gastral cavity. In Stage XI the proctodoeum still ends blindly.

<sup>&</sup>lt;sup>1</sup> See Appendix.

The cuticle which occurs during Stage XI over the free surface of the gastral epithelium is a definite membranous exuvia and not merely a condensation of the peripheral protoplasm (see Text-figure 6).

My observations on the endoderm of P. novae-britanniae may be briefly summarised as follows:

- 1. In Stage VIII many endoderm cells forsake their epithelial position and become converted into wandering trophocytes.
- 2. In Stage X the endoderm commences to reconstitute itself. The trophocytes tend to become less numerous, either being absorbed or applying themselves to the basal membrane, which has been secreted by the endoderm cells concomitantly with the separation of the inner and outer germ-layers to form the definite body-cavity. The endoderm may be said to contract away from the ectoderm.
- 3. In Stage XI the endoderm cells have increased in height and secreted a cuticular membrane, and now constitute a fairly compact epithelial layer containing numerous eosinophile globules of varying sizes. The proctodoeum does not yet open into the gastral cavity.
- 4. In Stage XII the endoderm commences to undergo histolytic changes, the cuticle ruptures and the globules tend to loosely fill up the gastral cavity. todoeum now opens into the latter.
- 5. In young individuals the brightly staining globules have entirely disappeared. The endoderm does not form an epithelial layer, but consists of cells lying loosely and freely in the gastral cavity like the trophocytes in the embryo. Faintly staining minute spherules may be present.

The production of trophocytes may be looked upon as a partial histolysis, so that one histolytic change with subsequent reconstitution of the endoderm is at least an Then appear the yolk-like globules in the endoderm, and then comes a observed fact. These are also observed facts. What I have not observed is the second histolysis. reconstitution of the endoderm after this second histolysis. The reconstitution might not occur—assuming that it would occur—till months after birth. To definitely establish the existence of a periodic phenomenon, such as I suppose this histolysis of the endoderm to be, periodic observations are required, and these are at present lacking, with no immediate prospect of the want being met, and this must be my excuse for the imperfection of the above remarks.

#### NUTRITION OF THE EMBRYO.

It is quite clear that the nutrition of the embryo is effected through the walls of the trophic organ or vesicle and that the ectoderm of the vesicle is physiologically comparable with—perhaps its function is identical with—the peripheral ectoderm or trophoblast (Hubrecht) of the Mammalian blastodermic vesicle.

The trophic organ occupies at first the entire dorsum of the embryo, beyond which it projects freely in front as the head-fold, and behind as the tail-fold. As growth proceeds the caudal or growing end of the embryo emancipates itself from the wall of the vesicle, although the cavity of the latter is directly continued into the caudal or abdominal region as it increases in length and independence. After the appearance of the cephalic flexure (Stage IX), the trophic organ gradually decreases in relative dimensions until it is finally completely reduced to its definite proportions as part of the body of the animal.

In its capacity of dorsal trophic organ, the trophoblastic vesicle of the embryos of *P. novae-britanniae* is therefore comparable with the stalk of the embryo of the Neotropical Peripatus.

The stalked embryos of P. torquatus and edwardsii (=trinidadensis) were discovered and described by Kennel in 1886, and the discovery was confirmed by W. L. Sclater (17) in 1888. The two authors however differed considerably in their interpretation of their observations. Both agreed that the embryo is attached by a dorsal stalk to the inner wall of a closed vesicle. The embryo therefore lies inside the vesicle as in a brood-chamber. Kennel described the vesicle as being derived from the uterine epithelium which entered into relations with the embryo and rounded off at the ends to form a closed chamber. Sclater described the wall of the vesicle as a pure and simple derivative of the embryonic ectoderm, the cavity of the vesicle being produced by separation of the inner and outer layers of the so-called pseudogastrula, as in the Mammalian embryo. The figures given by Kennel and Sclater are remarkably alike, only they differ in their statements as to the relative ages of embryos. On the whole there are fewer gaps and fewer unique phenomena in Sclater's than in Kennel's description. In P. novae-britanniae there is no question as to whether the vesicle is an embryonic or uterine derivative. It is of course an embryonic structure, and the embryo lies outside and upon it, instead of inside it, as in the Neotropical species. Korschelt and Heider (13) summed up in favour of Kennel's interpretation. I think my results rather favour Sclater's conclusions.

In the embryo of *P. novae-britanniae* there is normally no space between the egg-membrane and the enclosed embryonic vesicle, but the membrane closely hugs the latter, and no doubt the vesicle in life is turgid and tightly pressed against the uterine wall. The uterine epithelium shows signs of great glandular activity with its vacuolar cells, and its inner surface is often raised up into small prominences caused by the artificial separation of the embryo from contiguity with the wall. The uterine epithelium is locally thickened in the neighbourhood of an embryo.

In P. capensis Sedgwick states that in normal embryos there is always a space between the embryo and the membrane filled with fluid, and in his Stages E to F the dorsal ectoderm is much thickened and vacuolated, especially in the region of the so-called dorsal hump, and probably, according to Sedgwick, has a nutritive function, absorbing the fluid in which the embryo lies.

In *P. novae-zealandiae* the dorsum of the embryo is occupied by yolk; and Miss Sheldon has described a peripheral layer of yolk or ectodermal yolk between the embryo and the egg-membrane, thus occupying the same position as the nutrient fluid in *P. capensis*.

In the Neotropical Peripatus the egg-membrane completely disappears before the close of the segmentation stages (Kennel 11, Sclater 17), and the embryo becomes applied against the uterine wall without any intervening membrane. In some cases (P. torquatus Kennel) circular ridges are developed on the outer wall of the vesicle

in which the embryo lies, which fit into corresponding depressions of the uterine wall. One such ridge was also figured by Sclater round the embryonic vesicle of the species investigated by him (P. imthurni = demeraranus). P. edwardsii = trinidadensis is without such a ridge (Kennel). It therefore appears that the various Neotropical species offer considerable differences inter se, in their development. The uterine wall of the Neotropical Peripatus appears to differ from anything that has been described in the other subgenera in that the thick wall of the uterus includes and is traversed by blood-spaces. These were described and figured by Kennel, and again figured by Sclater. Therefore I do not understand the following statement made by the latter author. He says "In the case of Peripatus imthurni (demeraranus Sedgwick), there is certainly, as far as I have been able to observe, no plexus of blood-vessels at all [in the uterine wall]: and Kennel, I think, makes no mention of this matter."

In this quotation the use of the word "blood-vessels" instead of "blood-spaces" is unfortunate. Kennel was also unfortunate in his selection of terms when he applied the term "placenta" to the mechanism by which the embryo acquires its nutrition.

# MORPHOLOGY OF THE TROPHOBLASTIC VESICLE OF P. NOVAE-BRITANNIAE.

While discharging its nutritive function, the trophic organ at the same time serves as a water-cushion for the protection of the embryo, like the amnion of higher Vertebrates (cf. Haddon quoted by Hubrecht 9). Thus the trophic organ has a double function, (1) that of nutrition and (2) that of protection of the embryo. The function of nutrition is its primary function while that of protection is quite a

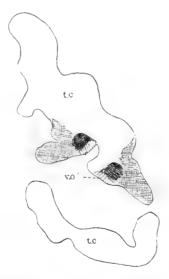


Fig. 7. Outline sketch of transverse section through the mid-region of the embryo shown in plate III, Fig. 35.

t.c. trophic cavity. v.o. thickened patches of ectoderm from which the nerve-cords are delaminated. These unite later to form the ventral organs.

secondary or accessory function. The amniotic folds of Insects are purely protective. Thus the primitively secondary function of protection has entirely superseded the original nutritive function. It follows from this view that the amnion of Insects is not a new acquisition of their yolk-laden eggs, but is the derivative of an original nutritive organ developed in correlation with an alecithal ovum.

The trophic organ of the embryo of P. novae-britanniae is analogous to a temporary larval structure—like the suckers of a tadpole. But unlike the latter it is not developed for use during an independent larval existence, but is essentially developed for use during intra-uterine development. When the embryo is flexed and the anterior portion of the trophic organ covers its ventral surface as with a cap (see Text-figure 7) the superficial resemblance to the amnion of an insect is remarkable—and this resemblance must, in principle, be still more remarkable in the case of those insects (certain Diptera, see Korschelt and Heider, p. 783) in which the amniotic folds do not fuse together, but remain as separate folds. This is the case, according to Kowalevsky and Graber (quoted by Korschelt and Heider) in the Muscidae "bei denen die Kopffalte äusserst rudimentär bleibt und nur die Schwanzfalte zu etwas deutlicherer Entwicklung gelangt. späteren Ausbildung des Embryos werden diese Falten einfach wieder ausgeglattet und nehmen dann, wie es scheint, an der Ausbildung der Rückenhaut einen gewissen Antheil." This is exactly what the trophic folds of the embryos of P. novae-britanniae do. In the latter, however, the anterior trophic extension or head-fold predominates considerably, through all stages, over the posterior or tail-fold. There is thus a temptation to suggest that, in addition to the superficial resemblance, there is a genetic relation between the trophic organ or trophic folds here described and the amniotic folds of Insects. And this I do tentatively suggest, on the same principle which led Hubrecht to reject the prevailing grossly mechanical explanation of the amnion of the higher Vertebrates, and to trace it back to a primitive trophic organ, the trophoblast (Hubrecht 9).

## LECITHALITY OF THE OVUM.

It is perhaps not always realised that the acquisition of yolk is as radical an innovation as that of any other kind of trophic organ for the nutrition of the embryo. The origin of yolk has been the subject of as much controversy as any other problem of embryology. Even now there seems to be no prospect of arriving at an agreement, not so much as to the origin of yolk in any concrete example, but rather as to the general principles which govern the acquisition and loss of yolk. The acquisition of yolk is an observed phenomenon within the limits of many groups of animals. The loss of yolk in any specified case is always an assumption or hypothesis.

I will not attempt to discuss this very difficult subject about which hardly any two zoologists hold similar opinions, but will merely point out how the question is affected by the phenomena of development observed in *P. novae-britanniae*. In

<sup>&</sup>lt;sup>1</sup> The figures of the embryos of Lepisma given by Heymons should be compared with those of the embryos of *P. novae-britanniae* accompanying this paper, so far as external appearance is concerned. According to Heymons, the amniotic cavity in Lepisma never completely closes during the period of its existence but has a permanent external opening, the amniotic pore (Amnionporus). [Richard Heymons. Entwicklungsgeschichtliche Untersuchungen an *Lepisma saccharina* L. Z. f. w. Z. Bd. 62, 1897, p. 583.]

P. capensis the egg, as shown by Sedgwick, is large and contains vesicular protoplasm. Sedgwick very naturally supposed that this indicated a loss of yolk which had formerly filled the vacuoles at present occurring in the egg—especially in view of the yolky egg of P. novae-zealandiae. The view that the egg of Peripatus capensis exhibits a stage in the process of acquiring yolk instead of being a stage in the loss of yolk, could be sustained with equal force. There is no means at present known of deciding between these two views in this particular case. Both of them seem to be equally possible. In the egg of P. novae-britanniae however, as well as in those of the Neotropical species of Peripatus, this difficulty is not present, since there is no reason whatever to suppose that there has been a secondary loss of yolk in these cases.

Yolk may be defined as reserve nutrient matter derived from the maternal organism and deposited in the egg in a sub-solid form. Fat is an analogous reserve food-stuff stored up by various animals for use in times of low-feeding or of cessation of feeding, and derived from foreign ingested nutrient matter.

As has been described above, in the late embryos of *P. novae-britanniae* at a time when they are approaching the period of birth, large and small globules of reserve nutrient matter—the eosinophile globules—make their appearance in the endoderm.

Whatever the chemical constitution of these globules may be, whether allied to fat or to lecithin, the fact remains that they are yolk-like globules deposited in the endoderm of the late embryos and derived, like true yolk, from the maternal organism. It thus appears possible that the early appearance of yolk in eggs which contain yolk is only a special case of the nutrition of the embryo at the expense of the maternal organism, and that reserve nutrient matter of a like nature, so far as function (i.e. nutrition of foetus) is concerned, may appear at a much later stage in the development.

The fact of these eosinophile globules making their appearance in the endoderm is of interest since the seat of yolk in eggs is essentially at the vegetative pole which later gives rise to the endoderm.

Thus it will be seen that within the limits of the genus Peripatus we are confronted with a problem with regard to the lecithality of the ovum, which is exactly analogous to that presented by the Mammalian ovum. I suppose many embryologists take it for granted that the yolkless condition of the ova of the higher Mammals is quite a secondary condition. It is therefore interesting to note that one of those best fitted to judge does not hold this opinion. I refer to Professor Hubrecht.

As for Peripatus all I can say, with the limited experience which I have had of this remarkable genus, is that it appears to me to substantiate the principle upon which Prof. Hubrecht's views are based.

# PHYLOGENETIC CONSIDERATIONS.

The fundamental differences in the early development of the four known subgeneric groups of Peripatus which at first appear to be so unaccountable, may, by their very diversity, afford a clue to the phylogeny of Peripatus.

This subject has been already speculated upon by Kennel.

With the knowledge available at the time Kennel wrote, he said that it seemed certain that within the limits of the genus Peripatus the method of embryonic develop-

ment had assumed two divergent directions whose extreme points are represented in the Neotropical and New Zealand species respectively.

The starting point, according to Kennel, was to be sought for in an ancestral form which discharged its small yolkless eggs directly into the water. The eggs would develop into free-swimming larvae which fed themselves independently. Concomitantly with the adaptation to a terrestrial life and the modification of organisation (e.g. development of tracheae) which rendered oviposition in water impossible, the oviduct assumed the rôle of a brood-chamber, as indeed in many other animals, e.g. Salamandra atra.

At first, says Kennel, it may well be assumed that the intra-uterine development was only slightly different from the free development; the embryos and larvae would be nourished by the uterine secretions as in *Paludina vivipara*, until finally all larval structures required for a free life completely disappeared. This condition is represented in *P. capensis*, although there is here, according to Kennel, no longer any identity with the ancestral form.

The rest of Kennel's conclusions on this subject are necessarily coloured by his interpretation of the embryonic vesicle of the Neotropical species, as being a uterine and not an embryonic structure (see above, p. 31). This does not however affect the principle of his views. Referring to the two divergent methods of development mentioned above, he says that in the one direction the nutrition of the embryo (at the maternal expense) would be relegated to earlier and earlier stages and limited to a shorter time, until finally a considerable quantity of nutritive yolk was collected in the egg itself, as in P. novae-zealandiae. In the other direction the embryos became practically parasitic and became applied to the mucous membrane of the uterus. This is indeed true of the Neotropical species and of P. novae-britanniae. In both cases the embryonic vesicle in life is obviously closely pressed against the uterine wall, in the former without the intervention of an egg-membrane, and in the latter with the egg-membrane separating the ectoderm of the trophic organ (i.e. the trophoblast) from the uterine epithelium. As far as our present methods enable us to judge, Peripatus must have had an aquatic ancestor, and its viviparous habit must have been preceded by an oviparous habit. Assuming the latter to be true, namely, that Peripatus had an oviparous ancestor, it is quite certain, to my mind, that the oviparity of P. oviparus Dendy, is a secondarily acquired habit and not in any way to be confused with the primitive deposition of alecithal ova.

The accumulation of yolk in the egg of *P. novae-zealandiae* would lead by a comparatively simple gradation to a secondarily acquired habit of oviposition on *terra firma*, the egg being provided with sufficient yolk for the nutrition of the embryo and surrounded by a protecting envelope or egg-shell. It is therefore a most interesting fact that this step has been taken by the Victorian species of Peripatus, recently described by Dendy as a distinct species, *P. oviparus* (Dendy 3).

In *P. oviparus*, according to Dendy's discovery, the yolky eggs are normally laid, and Dendy has succeeded in hatching out at least one embryo from such a deposited egg.

In P. novae-zealandiae the eggs are sometimes abnormally discharged, as observed by Hutton, but such precocious eggs do not develop further, so far as is known.

<sup>&</sup>lt;sup>1</sup> Kennel says they sucked on to the mucous membrane.

### TABLE OF COMPARISONS.

In the following table I have collected fourteen characters relating to the sexual and reproductive characters of the four known subgenera of Peripatus. It is thought that the presentation of these facts in a compressed form may be acceptable to the reader. (For other external characters, see the early part of this memoir.)

It is necessary to add a few explanatory notes to the table.

- i. I do not know whether the egg-membrane of *P. novae-britanniae* corresponds with the chorion or with the vitelline membrane of the Cape and Australian species. I think it corresponds with the chorion. It is possible that specially directed investigations might result in finding a thin vitelline pellicle below this membrane in the unsegmented ovum, or even during the early segmentation stages. It is certainly not present in my Stage III.
- ii. The egg-membrane persists beyond Stage X, but I have not found it in my oldest embryos. In *P. capensis* the chorion persists until birth (Sedgwick), as also in *P. leuckarti* (Steel).
- iii. In P. novae-zealandiae the young are white at birth, but the antennae are slightly tinged with purple (Hutton).
- In P. capensis the young at birth are either quite white or of a diffuse reddish colour; only the antennae are green (Sedgwick).
- iv. With regard to the mode of fecundation. At a meeting of the Linnaean Society of New South Wales, which I attended in Sydney in 1896, I heard Mr Steel describe copulation as occurring in *P. leuckarti*, but for some unaccountable reason the observation is not recorded in the paper by him which I have cited more than once. Its occurrence in *P. novae-britanniae* is rendered especially probable by the presence of the external muscular male papilla. Finally, it is a priori probable that it occurs in all, except in Peripatopsis, on account of the presence of a pair of specially differentiated receptacula seminis.
- v. Crural glands could not be included in the above table because, while they occur in *P. leuckarti*, they are absent from *P. novae-zealandiae*. As mentioned already, there are none in *P. novae-britanniae*.
- vi. Steel has observed that the young of *P. leuckarti* measure 5 mm. at birth, and during the first 12 months the rate of growth was rather less than 1 mm. a month. He estimates that a female takes upwards of two years to reach maturity, and thinks it probable that the birth of young does not commence until the mother is three years old.
- vii. It will be observed that the embryos of *P. novae-britanniae* and of the subgenus Peripatus s. str. are born in a more complete condition than are those of the other two subgenera. In other words, the viviparity is more complete. I should think the less complete viviparity of the latter forms is not a primitive feature.

| Appendages in \$\pi\$ and \$\delta\$  | Equal   | Equal                                      | Less<br>in &  | Less<br>in &  |
|---------------------------------------|---|--|---|---|
| Mode of<br>Fecun-<br>dation           | Probably by copulation                                  | Hypo-<br>dermic<br>injection               | Probably<br>hy<br>copulation  | Probably by copulation  |
| Spermato-<br>phores                   | Long,<br>thread-like                                    | Minute,<br>oval                            | Absent  | Long,<br>thread-like  |
| Ductus<br>ejacula-<br>torius          | Convolute   | Flexed                                     | Median  | Convolute   |
| Accessory Glands of $_{arsigme}$      | Open by paired apertures between genital pore and annas | Open into<br>Ductus<br>ejacula-<br>torius  | Open into median pygidial bulbas and then by median dorsal pore to exterior | Open by paired apertures beside the anus                                      |
| Receptacula                           | Absent  | Absent                                     | Absent  | Present   |
| Receptaculs                           | Present   | Absent                                     | Present   | Present   |
| Young at birth, Colour. Length in mm. | White<br>5. Steel                                       | White<br>10 15.<br>Sedgwick                | Pigment-Present<br>ed 15  | Pigment- Present Present ed 20-22. Kennel, Sedgwick                           |
| Uterine<br>Embryos,<br>Ages           |   | Uniform                                    | Successive  | Successive  |
| Nutrition<br>of<br>Embryo             | Lecithal Varying  | Ecto-<br>dermal                            | Trophic vesicle with external sessile embryo                                | Trophic vesicle with internal stalked embryo                                  |
| Ova-<br>rian<br>ova                   | Exo-<br>genous  | Exo-<br>genous                             | Exo-<br>genous  | Endo-genous   |
| Egg,<br>Contents                      | Yolk  | Vesicular Exo-<br>protoplasm genous        | Single, Granular Exo-<br>extensile protoplasm genous<br>persistent          | Single, Granular Endo-<br>undergoing protoplasm genous<br>early<br>resorption |
| Egg.<br>Membrane                      | Double.<br>Chorion<br>thick,<br>persistent              | Double.<br>Chorion<br>dense,<br>persistent | Single,<br>extensile<br>persistent  | Single,<br>undergoing<br>early<br>resorption                                  |
| Egg,<br>diam.<br>in<br>mm.            | 1.5   | Ϋ́   |   | <b>†</b> 0.   |
|                                       | Peripatoides<br>(Australasian)                          | Peripatopsis<br>(Cape)                     | Paraperipatus<br>(New Britain)  | Peripatus, s. str.<br>(Neotropical)   |

# BREEDING-PERIOD, PERIOD OF GESTATION, ETC.

The production of embryos probably takes place all the year round in P. novae-britanniae:—this is also probably the case with the Neotropical Peripatus, and Hutton found that P. novae-zealandiae produces young all the year round.

P. leuckarti according to Fletcher breeds through about  $\frac{3}{4}$  of the year, the most prolific period being the six months from October to March. As a general rule it does not breed during the winter months (May—August), and in this respect differs markedly from the New Zealand species.

There is no means of determining the period of gestation except by periodic observations. In *P. leuckarti* Fletcher estimates it at 6—7 months. In *P. capensis*, as shown by Sedgwick, the period of gestation is 13 months; longer than in any Mammal. The fertilised ova pass into the oviduct in April and the young are born in May of the following year (Sedgwick). The period of incubation observed by Dendy in a deposited egg of *P. oviparus* was 17 months. That is to say, one of the eggs laid in his vivarium in Melbourne hatched out after an interval of a year and five months.

In *P. novae-britanniae*, where the embryos are born in strict succession, only the one nearest the vagina in each uterus being ready for birth at one time, it is possible that the period of gestation for a given embryo is even shorter than in *P. leuckarti*. It would also appear probable that the extraordinarily long period of gestation in *P. capensis* is in correlation with the uniformity of the ages of the uterine embryos.

# CLASSIFICATION.

It is not to be expected that a new species of Peripatus would throw any fresh light on the systematic position of this delightful creature. Nevertheless a few remarks on this subject may not be out of place. Its relationships being obviously divided between the Annelida and the Arthropoda, its place in a separate Class of equal value with either of these groups would seem to be clear enough. Hatschek in his Lehrbuch regards the Onychophora as of equal value with the Arthropoda. The point upon which I wish to say a few words is with regard to the name of the Class to which Peripatus belongs rather than its position in the system. There is an objection to the name Prototracheata (or Protracheata as it was originally written). This was applied to one of Haeckel's theoretical groups, and the name was adopted by Moseley after his discovery of the tracheae. It is a good name and has done good service in embodying a notable conception. The objection to it arises from the fact that there are reasons for supposing that tracheae have had a polyphyletic origin. If the name be accordingly rejected on this account, shall a new name be invented or shall an old name be re-established? Assuming that the latter course be adopted, which old name should be revived, Malacopoda or Onychophora?

In an interesting paper on the classification of the Arthropoda, Kingsley (12) says he prefers to use the name Malacopoda rather than Onychophora because it is older than the latter, having been introduced by Blanchard in 1847. It is certainly the older name, but it was not given by Blanchard but by de Blainville in 1840. This

example illustrates the fatuity of adopting ordinal names simply on the ground of priority rather than on that of efficiency.

De Blainville's name was little more than a nomen nudum. It was H. Milne-Edwards who discovered the divarication of the nerve-cords in 1842<sup>1</sup>. But Grube's memoir on Peripatus, besides being the best work which had appeared on the subject prior to Moseley's discovery of the tracheae, is intrinsically a work of abiding merit.

Therefore, in my opinion, Grube's name, Onychophora, should take precedence of all existing names for the Class to which Peripatus is regarded as belonging.

In conclusion I have to acknowledge with gratitude the uniform kindness of Mr Adam Sedgwick, F.R.S., in lending me specimens of *P. novae-zealandiae*, capensis, and balfouri for comparison, and in giving me the benefit of his experience of Peripatus. My thanks are also due to Mr J. P. Hill, B.Sc., for specimens of *P. leuckarti*.

Cambridge, May 17, 1898.

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   Theil II., Ibid., viii., 1888, p. 1.

<sup>&</sup>lt;sup>1</sup> Milne-Edwards (quoted by Grube) suggested the name Pleuroneura. Guilding had suggested Polypoda.

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#### APPENDIX.

- 1. References to the following authors have been added during the correction of the proofs:—E. L. Bouvier p. 3, L. Camerano p. 3, R. Heymons p. 33.
- 2. The occurrence of histolytic changes in the gastral epithelium of Peripatus, as described in the foregoing pages, is interesting in comparison with analogous phenomena which have been observed among the Myriapoda and Insecta as well as in other groups. I have found the use of the term gastrolysis to be convenient in this connection, as sarcolysis has been used in describing the fatty degeneration of the muscles of Insects. [C. de Bruyne. Recherches au sujet de l'intervention de la Phagocytose dans le développement des Invertébrés. Archives de Biol. xv. 1898, p. 181.]
- 3. Gastrolysis has been observed in the mid-gut of the scolopendroid genus Cryptops by Balbiani during the winter season. The epithelial cells had, at almost all points, detached themselves from the tunic of the gut and become transformed into an amorphous mass of granulations and refringent globules, which filled the cavity of the gut. The muscular tunic of the gut also underwent degeneration. "Ce processus de régression du tube digestif des Cryptops pendant la saison froide est à rapprocher des observations de Semper sur la chute de l'épithélium des Gastéropodes pulmonés pendant l'hibernation, et de celles de Sommer sur la mue de l'épithélium de l'intestin chez le Macrotoma plumbea [a Podurid]. On peut lui comparer aussi les phénomènes décrits par Kowalevsky touchant la destruction de l'appareil digestif chez les larves des Muscidés au moment de leur transformation en pupe." [E. G. Balbiani, Études sur le tube digestif des Cryptops. Archives de Zool. expér. (2) T. viii. 1890, p. 72.]
- 4. In the case of Peripatus, it is to be noted that during the gastrolysis, as described in the text, the tunic of the gut remains whole and intact.
- 5. Compare also the desquamative catarrh described in the stomach, intestine and pyloric appendages of Salmonidae by Gulland. [G. Lovell Gulland. The minute structure of the digestive tract of the Salmon, and the changes which occur in it in fresh water. Anat. Anz. xiv. 1898, p. 441.]
- 6. Further reference may be made to the paper by C. Rengel, Ueber die Veränderungen des Darmepithels bei *Tenebrio molitor* während der Metamorphose. Z. f. w. Z. Bd. 62, 1897, p. 1.
- 7. On the subject of eosinophile granulations and their relation to fat and yolk, see N. Bogdanoff, Ueber das Vorkommen und die Bedeutung der eosinophilen Granulationen. Biol. C. B. XVIII. 1898, p. 26.

# EXPLANATION OF THE PLATES.

#### PLATE I.

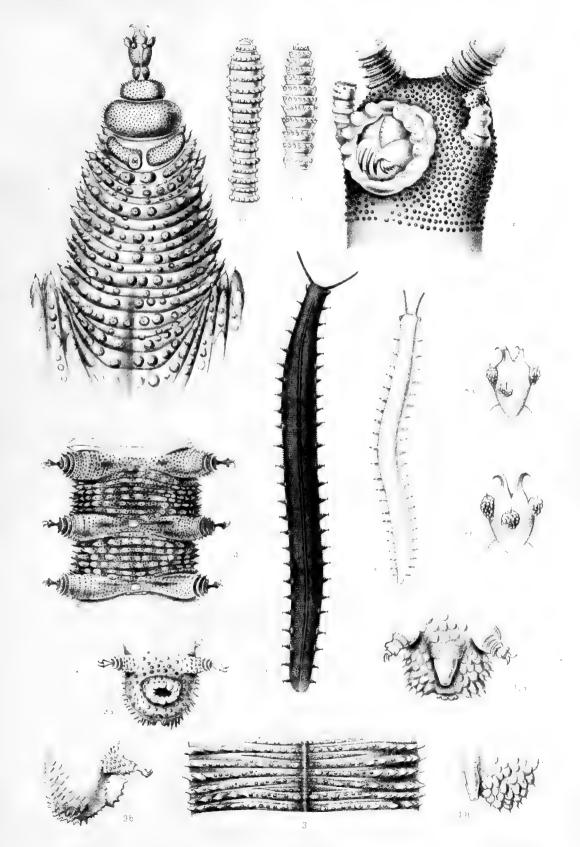
- Fig. 1. Adult female from dorsal aspect.  $\times 2$ .
- Fig. 2. Sketch of male,  $\times 4$ .
- Fig. 3. Enlarged view of portion of the back of the animal to show the interruption of the papilliferous ridges in the middle line; also the single row of papillae on each ridge. [In the Neotropical species the ridges usually carry a single row of papillae but they are not interrupted in the middle line. In the Cape and Australian species there is a median interruption but the papillae occur irregularly and in several rows (Sedgwick). The two species *P. tholloni* and *P. tuberculatus* recently described by Bouvier seem to be intermediate in this respect.]
- Fig. 4. Enlarged view of portion of the ventral surface. The papillae of the ventral surface differ from those on the dorsal surface in that they occur more irregularly, often in more than one row on the ridges. Among the more numerous smaller papillae are numbers of much larger papillae placed with considerable regularity in transverse rows and having a tubercular appearance when viewed with a lens. Similar tuberculiform papillae have been described by Bouvier on the dorsal surface of P. tuberculatus. The ventral organs are rendered prominent by their brown pigment.
- Fig. 5. Anterior end in  $\frac{3}{4}$ -ventral view, showing the characters of the jaws, the lips and the oral papillae. The modified appendages which carry the jaws are well shown and the fact that the jaws are homodynamous with the claws of the ambulatory appendages is well illustrated. The figure also shows the dorsal fleshy protuberance known as the "tongue" with its median row of chitinous denticles. Only the basal portions of the antennae are indicated. The oral papillae are characteristically flat-topped as if a slice had been cut off.

Figs. 6a and 6b. Free ends of the antennae of individuals of different ages to show intercalation of new rings between the older rings during the free life of the animal. Fig. 6a relates to a specimen 14.75 mm. in length, while Fig. 6b relates to one 54.75 mm long. The former had 33 rings in each antenna and the latter about 50.

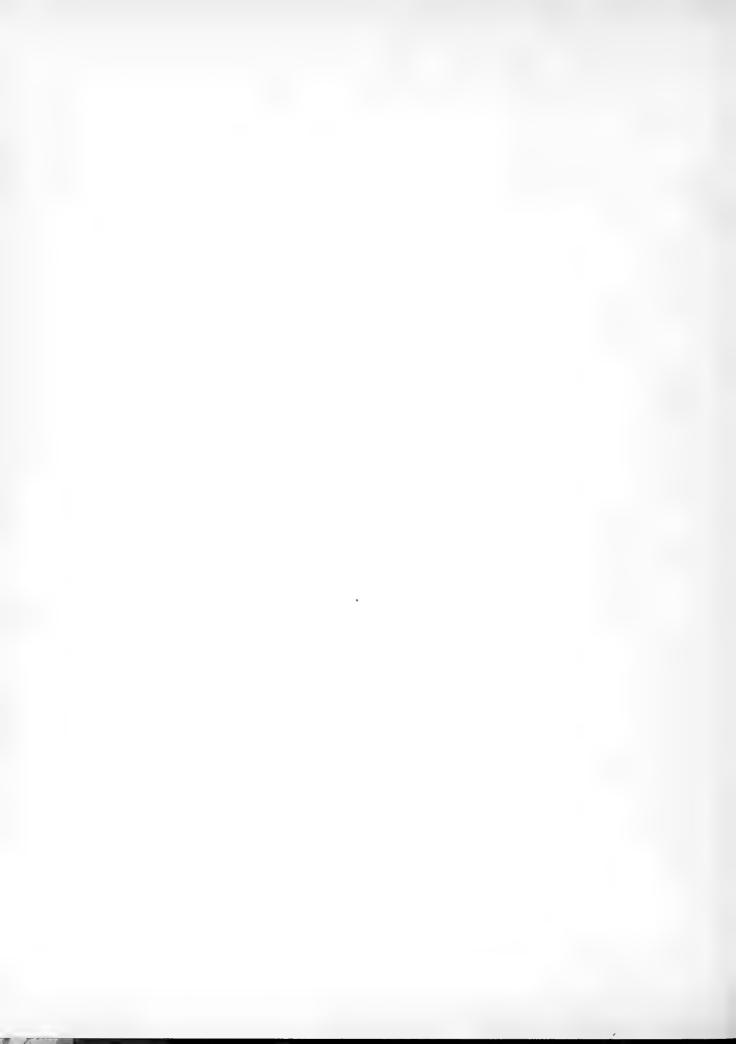
Fig. 7. Ventral view of an ambulatory appendage of the 4th or 5th pair. The external opening of the enlarged segmental organ is seen to occupy the centre of a prominent tuber-culiform structure which lies in the centre of the third spinous pad and causes an interruption in the continuity of the latter. The absence of primary papillae at the base of the "foot," i.e. at the insertion of the "pes" on to the "crus," is to be noted. In *P. capensis* there occurs a pair of primary papillae, the basal papillae, in that position.

Figs. 8a and 8b. Dorsal views of feet to show variation in the relative positions of the primary papillae. In Fig. 8a the dorsal papilla lies near the anterior papilla. In Fig. 8b the dorsal papilla is median.

Figs. 9a and 9b. Views of the posterior extremity of a female from the ventral and lateral aspects. The generative orifice with its tunid lips lies posterior to the last pair of legs. The anus is quite terminal.



Lower William Springs



Figs. 10 a and 10 b. Similar views of the posterior extremity of a male, showing the backwardly directed penis-like projection at the apex of which occurs the generative orifice.

#### PLATE II.

- Fig. 11. Ventral view of the 4th, 5th and 6th legs of the left side of an individual (I) in which each of these legs carried a peripheral nephridiopore.  $\times 10$ .
- Fig. 12. Dissection of female from above [specimen IV]. The posterior portion of each uterus is occupied by a pigmented embryo nearly ready for birth.
- a. anus. a.l.u. ascending left uterus. a.r.u. ascending right uterus. d.l.u. descending left uterus. d.r.u. descending right uterus. r.s. receptacula seminis. s.g. ramifications of slime-glands.
- Fig. 13. Posterior portion of same. The terminal portions of the two uteri have been cut across and the right uterus turned aside to the left, while the left uterus with the cohering ovarial organs remains in contiguity with the rectum.
- i. intestine. n.c. ventral nerve-cords beneath which the uteri have to pass before reaching the vagina.

Other letters as in Fig. 12.

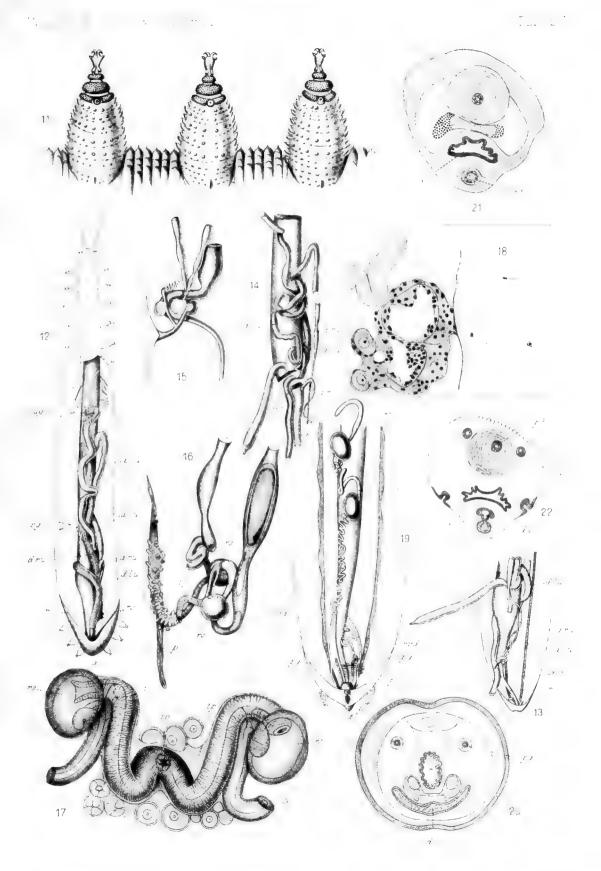
Fig. 14. Further view of same dissection. The uteri are partially unravelled. The ovary with the receptacula seminis as well as the greater portion of the ascending right uterus have been removed. Some of the uterine loops caused deep indentations in the wall of the gut.

int. intestine cut across to show the left uterus passing below it.

- Fig. 15. Ovary and adjacent structures from another female (VII). The ovary is attached to the pericardial septum. The ascending uteri loop round a bend of the descending right uterus. Only one of the proximal oviducal coils is shown; the other was concealed below the right uterus. This specimen measured 37 mm. in length; the uterine complex extended forwards 14.5 mm. from posterior end of body. The terminal portions of the uteri did not contain embryos.
- Fig. 16. Same removed from body. From a preparation in Canada balsam. The ovary, 1.5 mm. in length, is attached throughout its whole length to the floor of the pericardium, with the exception of a short erect posterior portion with which the infundibula communicate. The follicular character of the ovary is plainly indicated. The largest of the three embryos shown in the uterus to the right of the figure belongs to my Stage III and its length, including the chorionic membrane, was 1.1 mm.
- i. infundibula. o. ovary. p. pericardial septum (i.e. floor of pericardium). r. s. receptacula seminis.
- Fig. 17. Ovary and adjacent organs of young virgin female. This specimen (XI) was 17 mm. in length. Only a portion of the ovary is represented. The receptacula seminis were empty. The different appearance of that portion of each oviduct which precedes the receptaculum seminis from the succeeding portion is to be noted. Besides communicating with each other indirectly through the receptaculum seminis, these two portions of the oviduct, namely, the proximal or infundibular portion and the distal or uterine portion, communicate directly together by a short passage from one lumen to the other below and behind the

receptaculum seminis. This arrangement will be rendered intelligible by taking into consideration the mode of origin of the receptaculum seminis, as given on p. 11.

- i. infundibulum. i.o. common orifice of the infundibula putting latter in communication with the ovary. r.s. receptaculum seminis. t.p. peritoneal investment. u. uterus.
- Fig. 18. Transverse section through the ovary of a female embryo belonging to my Stage XI, to illustrate the exogenous growth of the ova. The ovary is attached in a sessile manner to the pericardial septum above which (in the figure to the right) the heart is seen in section, and below (at the upper left-hand corner of the figure) a portion of the wall of the rectum.
- Fig. 19. Dissection of adult male (V). The coiled vasa efferentia are succeeded by the uncoiled vasa deferentia which pass backwards to the posterior region of the body and then bend under the nerve-cords to meet in the mid-ventral line below the pygidial bulbus. The right genital duct passes below the intestine. Through a short portion of its course the rectum is held in position by a paired ligament (see Fig. 20). The convolute portion of the left pygidial gland is removed. The posterior extremity of the body is represented as being slightly tipped up to show the terminal organs.
- a. anus.  $\mathcal{J}$  penis. l.s.v. left seminal vesicle. l.t. left testis. l.v.d. left vas deferens. p.b. pygidial bulbus. p.g. pygidial gland. p.o. median dorsal orifice of pygidial glands. r.s.v. right seminal vesicle. r.t. right testis. r.v.d. right vas deferens. v.n.c. ventral nerve-cord.
- Fig. 20. Semi-diagrammatic section through a male (XII) taken immediately in front of the last pair of legs in the region where the nerve-cords (united by a commissure) approximate to one another before passing dorsally to meet together in the supra-rectal commissure. The rectum is held up by paired ligaments. The vasa deferentia meet below the nerve-cords in the median ductus ejaculatorius which is innervated (as is also the vagina) by a special pair of genital nerves whose roots are seen to project from the two ventral nerve-cords. The chitinous intima of the ductus ejaculatorius commences (or ends) slightly posterior to this point. The heart lying in the pericardium is shown dorsally.
  - d. e. commencement of ductus ejaculatorius. p. g. pygidial gland. r. rectum.
- Fig. 21. Similar section through same individual passing through the supra-rectal commissure. Above the latter lies the pygidial bulbus. The section is taken behind the last pair of legs.
  - d. e. ductus ejaculatorius. r. rectum.
- Fig. 22. Similar section through the anal segment, behind the supra-rectal commissure, to show the 5 ectodermal involutions mentioned in the text, namely 2 dorsal, 2 ventro-lateral and 1 median ventral lying over the ductus ejaculatorius. The ventral involution lies in the angle made by the insertion of the penis into the body-wall and is the ventral organ of the anal segment.
- d. e. ductus ejaculatorius immediately in front of the point at which it becomes emancipated from the body-wall to project freely as the penis. e. o. ectodermal organs. p. b. pygidial bulbus. r. rectum.





#### PLATE III.

- Fig. 23. Stage III in side view and optical section. The embryo is enclosed within the chorion (or egg-membrane) and consists of a large oval vesicle, the trophic vesicle, the wall of which is of uniform thickness except at the posterior ventral end of the vesicle where there is a much thickness area, the embryonic tract. Actual length of entire embryonic vesicle about 1 mm.
- Fig. 24. Posterior portion of an embryonic vesicle at a stage intermediate between Stage III and IV, in side view and optical section. Chorion omitted. The embryonic tract no longer abuts upon the posterior extremity of the vesicle, since the latter has begun to grow backwards to form the caudal extension of the trophic vesicle. Total length 1.45 mm. This embryo succeeded the preceding in the same uterus (specimen IV).
- Fig. 25. Stage IV. Portion of embryonic vesicle with embryonic tract, from the left side, showing the primitive (posterior) and cranial (anterior) grooves. The portion between these grooves, in comparison with the next stage, occupies the position of the future ventral surface of the embryo. Apparently the invagination which occurs in the next stage to form the definitive ventral surface proceeds from, or at least involves, the deeper posterior portion of the cranial groove. This embryo was taken from the same individual (VII) to which Fig. 16, Plate II relates. Total length 2.75 mm. Chorion omitted.
- Fig. 26. Stage V. Similar view showing appearance of a transverse groove in the middle of embryonic tract. This is the commencement of the formation of the ventral surface, or, in other words, it is the commencement of the ventral flexure, in situ, of the embryo. The embryo is not seen strictly in side view but in  $\frac{3}{4}$  side view, so that the cranial groove which separates the procephalic lobes is to be seen. This embryo comes from the same individual (IV) as those represented in Figs. 23 and 24. I have a permanent preparation in Canada balsam of this embryo. Chorion omitted.
- Fig. 27. Stage VI. Frontal view of an embryo in which the transverse groove seen in the preceding stage has taken a crescentic form owing to the forward free growth of the primitive streak. The latter now projects forwards like a tongue. The anterior portion of the trophic vesicle, or the trophic head-fold, is more extensive than the posterior portion, or trophic tail-fold. Embryo from specimen II. Total length 3.25 mm. Chorion omitted,
- Fig. 28. Enlarged frontal view of the embryonic tract of the same embryo. The centre of that portion of the embryo proper, which lies in front of the crescentic groove, is occupied by the cranial groove which is bounded by the first pair of somites, the outlines of which can be seen by transparency. The somites of the second pair lie at the outer sides of those of the first pair, while those of the third pair occupy a similar position with regard to those of the second pair. The dotted line indicates the plane through which the section represented in Fig. 51 was taken.
- Fig. 29. Stage VII. At this stage the primitive streak or caudal end of the embryo has by its continued growth become directed oblique-transversely, thus occasioning a superficial asymmetry in the entire embryo. The crescentic form of the embryonic tract, which is characteristic of the preceding stage, is still discernible. Owing to its oblique growth it is very difficult to describe the embryo in detail at this stage, and I have not attempted it. The overlapping of the mesodermal somites causes great complication. The features which

call for special notice are the caudal region of the embryo, the first pair of somites which have increased greatly in size, and lastly the relation of the embryo to the trophic vesicle.

Embryo from specimen IV. Total length 4.25 mm.

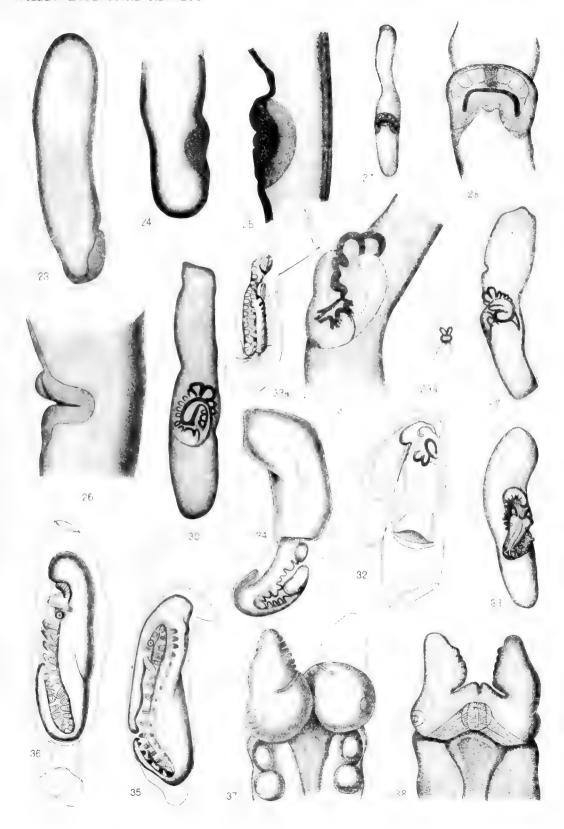
Fig.  $29\,a$ . Another embryo of the same stage with primitive streak directed quite transversely and so concealing all the somites, except those of the first pair, which occupy the procephalic lobes. This embryo immediately succeeded that shown in Fig. 27; when lying in the uterus the posterior end of its trophic vesicle abutted on the anterior end of the latter. Chorion omitted. From specimen II. Total length about 5 mm.

Fig. 30. Stage VIII. Frontal view. The caudal end of the embryo has grown to such an extent as to cause a double flexure in the embryo whereby the region of the primitive streak becomes directed backwards and a partial restoration of symmetry is the result. In embryos at this and the preceding stage, the two regions which can always be definitely recognised are the anterior and posterior extremities of the embryo. This is due to the characteristic shape of the caudal end and to the large size of the procephalic lobes with their contained somites of the first pair. Embryo from specimen II. Total length about 5 mm. Chorion omitted.

Fig. 31. Enlarged view of the same embryo from the left side. It is clearly shown here how the trophic vesicle occupies the dorsum of the embryo, and is therefore essentially a dorsal structure. The dorsal sides of the procephalic lobes are confluent with the wall of the vesicle. The margin of the body is lobed by the outgrowing appendages, only those of the left side of the embryo being seen, except that the right procephalic lobe shows through from the other side by transparency. The lobe, which closely hugs the left procephalic lobe, is the future manducatory appendage of the left side. This is followed by the future oral papilla of the same side. These two lobes can already be distinguished from the succeeding appendicular lobes. The recurved caudal region can be seen by focusing down, and it is indicated by a dotted line.

Fig. 32. Embryo belonging approximately to the same stage as preceding. It lies in an acute bend of the uterus. The anterior portion of the trophic vesicle, or head-fold, is considerably larger than the posterior portion, or tail-fold. The latter has apparently shrunk away somewhat from the chorion. From specimen VII. As in other species, so in *P. novae-britanniae*, the uterus is constricted at intervals, but the intervals are not regular and the constrictions are not always adapted to the position of the embryo. It is not uncommon to find an embryo tightly squeezed by a uterine constriction. On the other hand, it is still more common to find two or more embryos placed end to end without any intervening constriction.

Fig. 33. Stage IX. The caudal and abdominal regions have now increased so much in their independent growth that the caudal extremity lies in front of the head. It is only the cephalic half of the embryo which is in direct continuity with the trophic vesicle. All that portion of the posterior part of the body which in the figure is seen to lie in front of the head is free from the trophic vesicle and only lying upon it as on a cushion. The cephalic extremity, with the procephalic lobes from which the antennae have begun to bud out, still occupies its primary position, and, when lying in the uterus, points in the direction of the vagina. The small circles, some distance behind the antennae, represent the manducatory appendages showing through by transparency. Chorion omitted. Total length upwards of 4 mm. Although the total length of the embryonic vesicle is somewhat reduced in this stage, the size of the embryo itself is much greater. This is a natural consequence of





the fact that, pari passu with the growth of the embryo, a decrease in the size of the trophic vesicle supervenes. From specimen II.

Fig. 33 a. Another embryo closely similar in point of age to the preceding. This figure is inserted chiefly for the purpose of elucidating the preceding figure and the remarks made upon the latter. It shows the independence of the posterior abdominal region. The trophic vesicle is only directly connected with the anterior abdominal and cephalic regions. The knob-like or funnel-like stomodoeum (the dark-shaded body behind the antennae) projects vertically into the trophic cavity. The embryo is doubled up by a ventral abdominal flexure, and the caudal end projects far in front of the cephalic end. The trophic vesicle is restricted to the anterior moiety of the embryo of which it forms the back. Thus in this region the wall of the trophic vesicle is the dorsal side of the embryo. The trophic cavity is continued into the free posterior moiety of the embryo, but its proportions are so narrowed that the dorsal side of the embryo in this region is not inflated as it is in the anterior region. The ventro-lateral margins of the body are thickened by the appendicular outgrowths which contain mesoderm and by the delaminating nerve-cords. The latter appear as distinct parallel ridges bounding the sides of the body. Between the neural ridges the ventral body-wall is as thin as the wall of the trophic dilatation, so that between the neural ridges there is a wide longitudinal groove which is seen very clearly by focussing deeply through the trophic wall. This explanation will account for the appearance of a notch in the figure at the point of flexure of the embryo. The parallel neural ridges are shown in the anterior region, but only the left ridge can (from this aspect) be traced round the bend and along the recurved abdominal region; the right neural ridge becomes quite concealed beyond the bend. Only the appendages of the left side are indicated, although those of the right side showed through by transparency. (See Fig. 7 in the text for illustration of the internal groove between the neural ridges.) From specimen IV.

Fig. 34. This is an exceptional embryo which in some respects is less advanced than the preceding, and in other respects more advanced. Thus the antennae have not yet budded out from the procephalic lobes and the lips have not commenced to enclose the manducatory appendages, but the trophic vesicle has almost entirely disappeared from the region of the trunk, and appears as a relatively enormous lobe springing from the head. Near the point of abdominal flexure of the embryo there is still a trace of the posterior portion of the trophic organ. The curious way in which this posterior remnant of the vesicle is bent up is due to the fact that at that point the embryo was caught in a sharp bend of the uterus like that shown in Fig. 32.

In addition to the abdominal flexure there is the same caudal flexure which has been noticed in previous embryos. Chorion omitted. From specimen III.

Fig. 35. Stage X. In this stage the embryo has advanced considerably from the condition observed in Stage IX. The caudal flexure has disappeared, or, in other words, the tail has straightened out, and the point at which the abdominal flexure occurs has receded backwards, so that the posterior end of the body now lies a long distance behind the head. Meanwhile a cephalic flexure has occurred, so that the anterior end of the embryo is bent backwards and does not point towards the vagina. The trophic vesicle is much reduced relatively to the size of the embryo, but a long and very remarkable prolongation of the vesicle extends beyond the head, covering over the ventral surface of the embryo. The first appendage seen behind the antenna is the oral papilla. The embryo is shown removed from the uterus, but enveloped by the chorion. From specimen IV. × 12.

- Fig. 36. Portion of uterus containing an embryo of about the same stage as the preceding, but varying considerably in appearance. For some reason or other the cephalic flexure has not taken place, so that the antennae still point towards the vagina (i.e. away from the ovary) as in earlier stages. The trophic vesicle is still more reduced than in the preceding embryo. There is no prolongation of the vesicle overlapping the ventral surface, but merely a prominent lobe in front of the head. The antenna is seen to arise from the prominent procephalic lobe behind which is the oral papilla of the left side. The manducatory appendages, being already enclosed, are not to be seen. Behind the base of the procephalic lobe is to be seen a small knob-like structure projecting dorsally and slightly backwards into the interior of the embryo. This is the stomodoeum. The abdominal flexure has not receded back so far as in the preceding embryo. From specimen VII. × 12.
- Fig. 37. Enlarged view of the head of the embryo shown in Fig. 33; 'from the ventral side. The vestibule leading into the stomodoeum is so deep that the latter cannot be seen in this view. The antennae arise by a narrow base from the procephalic lobes; at the sides of the latter are to be seen the optic vesicles. Behind the procephalic lobes, the lips are beginning to surround the manducatory appendages, and behind these are the oral papillae.
- Fig. 38. Dorsal view of same. The stomodoeum is seen to lie immediately below the dorsal integument; its lumen is seen in optical section; the lines radiating from it no doubt represent the retractor muscles. From its position with relation to the procephalic lobes it will be readily inferred that it projects dorsally and forwards. At a later stage (Fig. 36), as we have seen, it projects dorsally and backwards, and at a still later stage, as in the adult, it projects backwards. Thus is illustrated what I have described as the rotation of the stomodoeum. At an earlier stage than the present the stomodoeum projects straight forwards (see next Plate).

#### PLATE IV.

As the chief object of the figures on this plate is to assist in the elucidation of the embryos represented on Plate III, it was not thought necessary to fill in the histological details. The outlines were drawn with the camera lucida from sections  $5\,\mu$  thick cut transversely to the long axis of the embryonic vesicle. The layers are indicated by different tints, the dark tint denoting ectoderm, and the lighter tint the mesoderm and endoderm. Where the endoderm is clearly distinct from the mesoderm, it is differentiated from the latter by a still lighter tint.

The trophic vesicle in the fresh embryo is distended with nutrient fluid contents, and, after preservation, its walls appear more or less collapsed according to the relative rapidity with which the diffusion between the contents of the cavity and the preserving fluid has taken place.

### Figs. 39, 40. Stage III.

Fig. 39. Posterior region of embryonic tract with primitive streak and primitive groove.

Fig. 40. Anterior region of primitive streak (seven sections from preceding) with overlying cranial groove. The thickened ectoderm of the embryonic tract passes gradually into the simple trophic ectoderm. In this embryo the wall of the trophic vesicle had collapsed, so that its cavity appears much reduced.



Flat Aller Seleta



#### Figs. 41-45, Stage IV.

- Fig. 41. Posterior region of embryonic tract behind the primitive streak. The section involves the hinder end of the mesodermic proliferation. Shortly behind this region the thickened cap-like plate of embryonic ectoderm ceases, and the wall of the trophic cavity consists simply of trophic ectoderm and trophic endoderm.
- Fig. 42. Hinder portion of primitive streak (five sections intervening between this and preceding).
- Fig. 43. Middle portion of primitive streak with shallow primitive groove. This is not quite the deepest portion of the groove.
- Fig. 44. Middle region of the embryonic plate in front of the primitive streak, between the latter and the cranial groove. The solid plate of mesoderm occupies the whole width of the embryo between the thickened embryonic ectoderm and the endoderm.
- Fig. 45. Anterior region of embryonic plate. The mesodermic plate is here seen to be dividing into paired mesodermic bands which are still united together across the middle line by a narrow bridge. The separation of the mesoderm into paired bands coincides with the depression caused by the deepening by the cranial groove. At this stage the stomodoeal involution cannot be distinguished from the cranial groove.
  - Figs. 46-50. Another embryo of the same stage, being the one shown in Fig. 25.
- Fig. 46. Posterior end of primitive streak. The mesodermic mass attains the surface of the embryo and appears as a plug between the two portions of the embryonic ectoderm which meet together behind this point. The embryonic vesicle is seen lying within the chorion which is omitted from most of the drawings.
- Fig. 47. Middle region of primitive streak with groove. This is practically identical with Fig. 43.
- Fig. 48. Anterior end of primitive streak. This section passes through the deepest part of the primitive groove which forms at this place, at a later stage, the proctodoeal involution.
- Fig. 49. Region of cranial groove. This groove extends over some seven or eight sections; its depth varies slightly at different points.
- Fig. 50. Anterior region of embryo in front of the cranial groove. A solid tongue of ectoderm reaches the endoderm and completely divides the mesodermal bands from one another. In comparison with the next stage this tongue may represent the delamination of the stomodoeum, or it may merely be related to the base of the cranial groove. In front of the region represented by this section the embryonic plate rapidly dwindles out, and only the trophic ectoderm and endoderm remain.
  - Figs. 51—57. Stage VI. Sections through the embryo represented in Figs. 27 and 28. W.

Fig. 51. Section passing through the middle of the primitive streak which has begun to double over the ventral surface of the embryo and become independent of the trophic vesicle. The embryonic ectoderm is coextensive with the mesoderm which, at this stage, is rapidly breaking up into hollow somites. Beyond the dorsal edge of the somites (on the lower side of the figure) the embryonic ectoderm passes sharply into the trophic ectoderm which can be easily distinguished in all sections by the character of its cells. Beyond the frontal or ventral edge of the somites the thickened lateral ectoderm passes into the low ectoderm which now occupies the ventral surface of the embryo proper. The primitive groove occupies the median ventral line of the primitive streak, its position being apparently reversed from that of previous stages in consequence of the recurvature of the free growing end of the embryo. Thus in previous stages the primitive groove faced outwards, now it faces inwards. The section may have been slightly oblique since two somites are seen on the left side of the figure, namely, somites 3 and 4, while only somite 4 is seen in section on the right of the figure. The primitive streak as here figured is essentially identical with that of P. capensis as figured by Sedgwick in his Stage C. It is quite solid and consists of a mass of proliferating cells in which may be distinguished an outer portion or mes-ectoderm and an inner core or mes-endoderm, the latter proceeding from the former. The chorion is shown in the figure.

Fig. 52. Section passing through the plane in which the outgrowing caudal region unites with the main body of the embryo. This region lies posteriorly to the preceding with relation to the cephalic end of the embryo, but a little reflection will show that the superincumbent caudal portion of the embryo is morphologically anterior to the free primitive streak of Fig. 51. We have in fact got beyond the primitive streak. The somite to the right of the figure is the anterior portion of the fifth somite (counted, of course, from the head); that to the left is the posterior portion of the fourth somite. This obliquity may be merely due to an accident of cutting or it may be partly due to a slight inequality in growth. The irregular cavities in the mes-endodermic mass are portions of the trophic cavity and their appearance is due to the fact, that, so far as the caudal portion of the embryo is concerned, the section cuts the caudal mesoderm tangentially.

Fig. 53. Section passing through the tail-swellings with nascent somites. This section is posterior to the preceding, that is to say, nearer the posterior end of the trophic vesicle, but it is easy to understand that the nascent caudal somites are approaching the trunk-somites. The conditions here portrayed are at first rather puzzling, but they are due to the fact mentioned in the text that the flexure of the embryo occurs in situ. The trunk-somite to the right of the figure is the anterior tip of the sixth somite; that to the left is the middle of the fifth. Behind this region the tail-swellings gradually flatten out until finally the embryonic region is passed over and we find as before merely trophic ectoderm and endoderm.

Fig. 54. Section passing tangentially through the posterior portion of the "head-swellings." It shows the transition from the thin ectoderm of the ventral abdominal surface into the thickened ectoderm of the cranial groove and cephalic region generally and also the entrance to the stomodoeum. On the right of the figure, somites 3 and 4 are seen in section, and to the left somites 2 and 3. This section passes through the posterior margin of the cephalic region which forms the anterior limit of the crescentic groove shown in Figs. 27 and 28.

- Fig. 55. Section passing immediately in front of preceding showing the minute lumen of the stomodoeum enclosed within the thickness of the ectoderm at the base of the cranial groove. Only ectoderm is shown in the figure.
- Fig. 56. Section passing slightly anterior to preceding showing the solid anterior end of the stomodoeum lying below the cranial groove. The somites on the right are 1, 2 and 3; those on the left, 1 and 2.
- Fig. 57. Section through anterior region of embryo in front of the stomodoeum. The embryo proper is as usual restricted to the ventral (upper in the figure) moiety of the trophic vesicle. As before, the embryonic ectoderm merges into the trophic ectoderm at the level of the outer and dorsal margins of the somites. The figure gives a good impression of the relatively enormous capacity of the trophic vesicle. Somites as in preceding.
  - Figs. 58-65. Stage VIII. Sections through the embryo represented in Figs. 30 and 31.
- Fig. 58. Through middle of procephalic lobes with first pair of somites, in front of stomodoeum. The outline of the trophic vesicle is rendered diagrammatically. At the outer angles made by the procephalic lobes with the trophic vesicle, the embryonic ectoderm passes into the trophic ectoderm.
- Fig. 59. Section somewhat posterior to preceding passing through the stomodoeum which in this stage has a well-defined lumen and runs straight from behind forwards as a caecal tube below the cranial groove. The section cuts the lobes which give rise to the manducatory appendages, tangentially. The shallow groove on the outer side of the procephalic lobe (only shown on the right of the figure owing to slight obliquity) occupies the position of the optic vesicle and is no doubt to be interpreted as the optic groove.
- Fig. 60. Section through the posterior end of the procephalic lobes showing the stomodoeum fused with the ectoderm; also passing through the second pair of somites.
- Fig. 61. Section immediately behind the procephalic lobes (on the left one of them is cut tangentially) through the external opening of the stomodoeum. On the left is somite 2; on the right somites 2 and 3. In somite 2 on the left there is a short canalicular portion of the somite bounded by the somatic mesoderm and opening into the cavity of the somite. This presents, in the preparations, the appearance of being a vestigial segmental organ.
- Fig. 62. Section through the third pair of somites. On the right a small portion of the 4th somite is involved in the section. The segmental tubules of the third pair of somites have commenced to form and one of them is shown to the right of the figure, as a small tube enclosed in the somatic mesoderm, and shut off from the main cavity of the somite. In front of this point the tubule opens freely into the latter; behind it ends blindly.

The trophic ectoderm is indicated by the dotted lines.

Fig. 63. Threefold section of embryo due to the double flexure—abdominal and caudal. Trophic ectoderm is indicated by dotted lines. The lower section is through the caudal region, that on the left through the abdominal region and that on the right through the anterior region at the level of the fifth somite.

The trophic ectoderm accompanies the abdominal flexure but not the caudal flexure. It enables the dorsal side of the embryo to be distinguished.

### 52 THE ANATOMY AND DEVELOPMENT OF PERIPATUS NOVAE-BRITANNIAE.

Fig. 64. Similar section farther back. In the middle of the thickened ventral surface of the caudal portion of the section is shown the proctodoeal involution.

Fig. 65. Section through the plane of junction of the abdominal and anterior regions. It passes through the angle of flexure. The ventral surfaces are seen to be united, the flexure being a ventral one. Trophic ectoderm denotes the dorsal side of the embryo and is indicated by dotted lines. The lower independent portion of the section passes through the region of the primitive streak which is now much reduced from the condition shown in Fig. 51. It now resembles the original condition seen in Figs. 42 and 47. In fact having nearly served its purpose it is on the way to disappear.

# METAPROTELLA SANDALENSIS, n. sp.

# BY DR PAUL MAYER.

THE Caprellidae which I recently received from Mr A. Willey, who requested me to describe them, all belong to the same species. There are 9 males, 5 females and 2 young individuals. Unfortunately almost all the legs had fallen off and the flagella of the superior antennae were broken.

The largest male measured fully 9 mm., not including legs and antennae; the flagellum of the superior antenna, so far as it was present, had 11 segments.



Fig. 1.

The species is new and belongs to the genus *Metaprotella*, Mayer (Mayer, Die Caprelliden des Golfes von Neapel, Nachtrag, 1890, p. 24). It may be named *sandalensis* after the place in which it was found, namely, Sandal Bay, Lifu.

Apart from the character of the mouth-parts, the most distinctive feature of the genus *Metaprotella* is the fusion of the last thoracic segment with the preceding segment (Fig. 1). In the arrangement of the spines, this species closely resembles *M. haswelliana*;

thus, the head carries a pair of spines dorsally and another spine on each side at the point of insertion of the mandibles; further on segment 2, there is a pair of dorsal spines and an unpaired spine at the hinder margin of the segment; the same applies to segment 3; finally in the male there is a pair of robust spines placed latero-ventrally near the anterior margin of segment 2. These latero-ventral spines of the second segment are reduced to mere knobs in the female.



Fig. 2.

The mandibular palp carries at the end between the two long bristles 8 or 9 short simple setae, and two short feathered setae (Fig. 2).



Fig. 3.

The palp of the maxillipede (Fig. 3) has an inwardly directed process at the distal end of the penultimate segment as in *M. haswelliana* and *M. excentrica*. For the rest, the mouth-parts are typically those of *Metaprotella*.

The rudimentary legs of the third and fourth segments are about half as long as the branchiae; they are slender, and provided at the end with one long and about six short setae—the latter somewhat damaged in the specimens.

The form of the first and second legs of an adult male is shown in Figs. 4 and 5, with regard to which it should be noted that the blunt teeth on the palmar margin

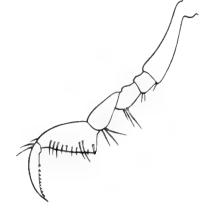


Fig. 4.

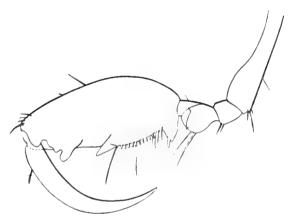


Fig. 5.

of the hand of the second leg (grosse Greifhand) vary considerably in number and appear also to be liable to fall off.

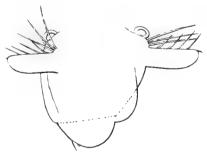


Fig. 6.

The abdomen of the male (Fig. 6) has only one pair of rudimentary appendages.

Habitat. Sandal Bay, Lifu, Loyalty Islands. They were taken, as Willey writes me, "chiefly from the tests of transparent Ascidians which attach themselves in great numbers to the native fish-baskets in from 10 to 15 fathoms of water."

The habitat of the new species is interesting. The other species of the genus Meta-protella have hitherto been found in Port Jackson (Australia), and also between Ceylon and the mainland of India and at the Philippine Islands. On the whole, as far as known, in the Tropics, compared with the higher latitudes, not only Caprellidae are rare but also the individuals are relatively small. This rule seems to hold good in the case of Lifu. As for the Equator, I stated years ago (op. cit. p. 99) that very likely in shallow water, on account of its high temperature, no Caprellidae whatever may live, and I should be very glad if investigators travelling in those regions or living there would state this assertion to be well founded.

Zool. Station, Naples. March, 1898.

#### EXPLANATION OF THE FIGURES.

- Fig. 1. Adult 3. × 8. The 3 last pairs of thoracic legs by which the animal hooks on to the Ascidian test, fallen off.
- Fig. 2. Tip of the mandibular palp. × 260.
- Fig. 3. Maxillipedes. × 180.
- Fig. 4. First leg-only the larger setae indicated. × 57.
- Fig. 5. Second leg-apparently somewhat shrunken. × 57.
- Fig. 6. Abdomen of of somewhat compressed. × 260.

## ON A LITTLE-KNOWN SEA-SNAKE FROM THE SOUTH PACIFIC.

### By G. A. BOULENGER, F.R.S.

#### With Plate V.

DURING his stay at Lifu, Loyalty Islands, Dr Arthur Willey was so fortunate as to secure two examples of a very rare marine Snake, which he has presented to the British Museum, where the species to which they belong was unrepresented. Although three descriptions of it have appeared, under as many different names, our knowledge of this Snake is a very meagre one, and it is therefore with great pleasure I accepted Dr Willey's proposal of drawing up an account, accompanied by figures, of the specimens obtained by him.

#### AIPYSURUS ANNULATUS.

Emydocephalus annulatus, Krefft, Proc. Zool. Soc. Lond., 1869, p. 322, and Snakes of Austral. p. 92 (1869).

Emydocephalus tuberculatus, Krefft, ll. cc. pp. 322, 93.

Aipysurus chelonicephalus, Bavay, Mém. Soc. Linn. Normand. xv. no. 5, 1869, p. 34.

Aipysurus annulatus, Boulenger, Cat. Snakes, III. p. 304 (1896).

Eye as long as its distance from the mouth. Snout short, rounded, twice as long as the eye; rostral as deep as broad, bearing a conical, spine-like tubercle suggesting the egg-wart or rostral callosity of some reptilian and batrachian embryos<sup>1</sup>; nasals longer than the præfrontals; frontal hexagonal, longer than broad, as broad as the supraocular, as long as its distance from the rostral; parietals as long as the frontal, sometimes divided by a longitudinal suture; supraocular undivided; nasal forming a suture with the single præocular; two postoculars; temporals 2+2; two upper and two lower labials, the second extremely large, formed by the fusion of several shields; first upper labial in contact with or narrowly separated from the præocular; two or three pairs of chin-shields, the anterior extra pair, if present, small, detached from the first pair of lower labials. The upper head-shields may be rough with small granules. Scales in 17 rows, feebly imbricate, nearly as long as broad, rough with several small tubercles. Ventrals 139—141; subcaudals 31. The coloration is different in the two specimens, both males:—

A. (Total length, 760 millim.; tail, 110.) Annulate black and yellow, the black annuli broader than the yellow ones and often running together on the middle of the back, and with some black spots between them on the belly; head yellow with a wide-meshed black network.

<sup>1</sup> Which is, however, absent in the sea-snakes as well as in all known Ophidians.

B. (Total length 690 millim.; tail 105.) Blackish brown, speckled with yellow on the sides and beneath, here and there with small yellow spots showing, in their arrangement, traces of the annuli described in the preceding specimen; head yellow, spotted and speckled with black.

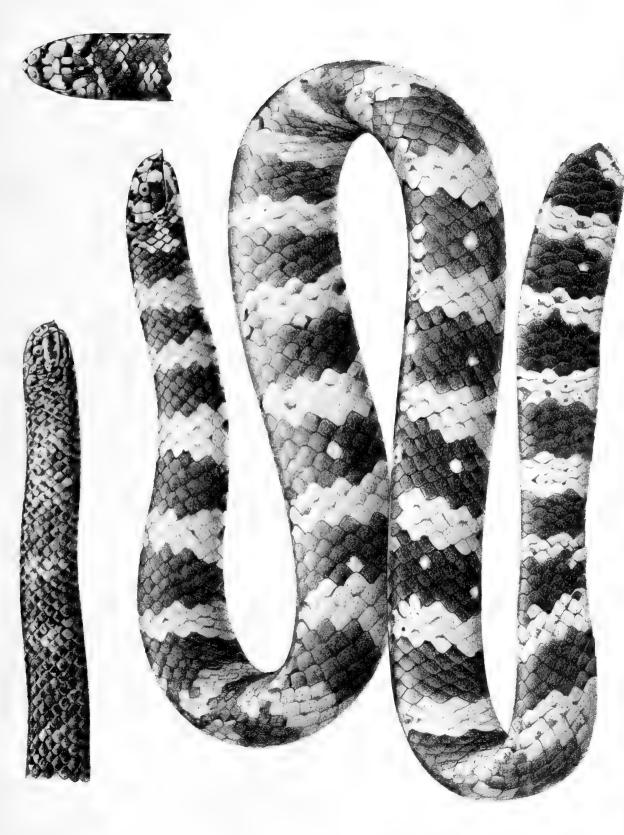
This species appears to have been described, almost simultaneously, by Krefft and by Bavay. The specimens obtained at Lifu by Dr Willey are unquestionably referable to Bavay's species, established on examples from the same locality and agreeing in the conical shape of the rostral shield. As to the Snakes, of unknown origin, described by Krefft, Mr E. R. Waite, of the Sydney Museum, has been so kind as to supplement, at my request, the insufficient account of them given by that author. Mr Waite agrees with me that *Emydocephalus annulatus* and *E. tuberculatus* are "undoubtedly the same," and he adds the following notes on their head-shields: "Rostral a little deeper than broad, with a groove on each side running from the mouth to the nasal. Frontal slightly longer than broad, not so long as its distance from the snout. Nasal broadly in contact with the single præocular. Three pairs of chin-shields, first smallest, the last separated by a shield."

These notes, together with a sketch of the head, upper and side views, taken from one of the types (that of E. tuberculatus), show a remarkable agreement with Dr Willey's specimens, except for the absence of the conical tubercle on the rostral shield. However, the fact that the degree of development of this tubercle varies in the Lifu specimens according to Bavay ("plus ou moins prononcée selon les individus") renders it doubtful whether this character by itself can be regarded as indicating specific difference, and I think it advisable to consider, provisionally at least, the specimens with and those without the tubercle as pertaining to a single species. This view is further substantiated by the remarkable agreement in the number of ventral and subcaudal shields, viz. 135—144+30—36 in Krefft's two specimens, and 144+36 in Bavay's type; whilst our two specimens show 139—141+31. As regards coloration, our specimens represent A. annulatus, Krefft (A) and A. tuberculatus, Krefft (B), whilst A. chelonicephalus, Bavay, appears to be exactly intermediate between the two.

<sup>1</sup> A trace of this groove is observable in our specimen B.

#### EXPLANATION OF PLATE V.

Aipysurus annulatus. Natural size, with upper view of head; and side view of head and anterior part of body of smaller specimen (B).



BOULENGER, AIPYSURUS ANNULATUR.

J. Species on real little

the right side being independent of and disconnected from that of the left. But in Gonibregmatus each mandible consists of an outer and of an inner branch, the former corresponding to the normal biting mandible of the rest of the class. The inner branch is united to its fellow of the opposite side, though the junctional suture persists, and the plate that results from the union constitutes physiologically a lower lip or labium designed presumably to prevent the escape of fluids issuing from wounds inflicted by the outer branches of the appendage. The mouth lies some distance behind the tip of this lower lip or labium and of the upper lip or labrum, and these two structures constitute the upper and lower walls of a channel which is closed at the sides by the outer branches of the mandible; the mandibles, labium and labrum thus form a kind of proboscis along which the fluid tissues of prey flow or are sucked backwards to the mouth.

CLASS. CHILOPODA (Centipedes).

ORDER. SCUTIGEROMORPHA.

FAMILY. SCUTIGERIDAE.

(1) Scutigera maculata, Newp.

Ann. Mag. Nat. Hist. XIII., p. 96, 1844; Tr. Linn. Soc. XIX., p. 359, 1845.

Loc. New Britain.

The specific identity of the two specimens obtained by Dr Willey in New Britain must be regarded as doubtful. Both are of small size and more or less damaged.

This species has been formerly recorded from Australia.

ORDER. SCOLOPENDROMORPHA.

FAMILY. SCOLOPENDRIDAE.

GENUS. Scolopendra, Linn.

(2) Scolopendra metuenda, Pocock.

Ann. Mag. Nat. Hist. (6), XVI., p. 423.

Loc. Narowol, (Eddystone) Solomon Islands.

The type and hitherto only known example of this species was obtained in New Georgia, in the Solomon Islands, by the officers of H.M.S. 'Penguin.'

GENUS. Cormocephalus, Newport.

(3) Cormocephalus violacescens (Gervais).

Cormocephalus violaceus, Newport. Tr. Linn. Soc. XIX., p. 424 (1845). (Not violaceus, Fabr.)

Scolopendra violacescens, Gervais. Ins. Apt. IV., p. 275 (1847).

Cormocephalus brevispinatus, L. Koch. Verh. zool. bot. Ges. Wien. 1867, p. 248 (teste Haase).

Cormocephalus purpureus, Pocock. Ann. Mag. Nat. Hist. (6), XI., p. 127 (1893).

The name violaceus applied by Newport to this species is inadmissible for it, having been previously given by Fabricius to a South African member of the same genus. Gervais's name violacescens can consequently stand. I proposed the name purpureus for the species upon discovering that violaceus had to be transferred, but forgetting that there were already a couple of other names in use.

Dr Willey obtained examples of this species in the Loyalty Islands (Lifu and Uvea). It was recorded from New Zealand by Newport, and from Gayndah and Rockhampton in Queensland by Haase.

GENUS. Cupipes, Kohlrausch.

(4) Cupipes amphieurys, Kohlr.

Cupipes amphieurys, Kohlrausch. Arch. Nat. 1882, p. 79.

Cupipes quadrisulcatus, Meinert. Amer. Phil. Soc. p. 187, 1885.

Loc. New Britain—a single specimen. Previously recorded from Ponape in the Caroline group.

GENUS. Otostigmus, Porat.

(5) Otostigmus punctiventer (Tömösv.).

Branchiostoma punctiventer, Tömösvary. Termes. fuzetek. IX., p. 66, pl. III., figs. 17, 18.

Otostigma punctiventre, Haase. Abh. Mus. Dresden, p. 72.

Colour olive green or nearly black, with metallic purple or bronze reflections; head, maxillipedes, first and last tergites tinted with chestnut red; legs a greenish or pale purple, paler at the base or indistinctly annulate; antennae greenish.

Head and maxillipedes punctured; coxal processes of maxillipedes with 3-3 or 4-4 teeth, the external on each side strong and separated, the internal fused.

Antennae 18-22 segments, whereof the basal two are naked.

Tergites from the 5th bisulcate, from the 9-11 marginate; from about the 5th or 6th covered with fine spinules, which increase in coarseness in the posterior half of the body; external portion of tergites distinctly though not very strongly wrinkled.

Sternites bisulcate in their anterior half, with a stronger or weaker posterior median impression; punctured and beset with short scattered setae.

Anal tergite and sternite spicular like the rest; the former mesially impressed posteriorly, the latter emarginate: pleurae elongate, armed with 5, 6 or 7 spines, 2 apical, 2 or 3 external, and 2 or 1 dorsal: anal legs long and slender, femur armed with about 14 spines, 3 (one apical), 3, 3, 5 or 4; protarsus with a spur. Rest of the legs also with protarsal spur. Length 50 mm., of anal leg 14.5, of antennae 15.5.

Loc. New Britain. Several specimens.

Haase's description of *O. punctiventer* from Sarawak, Borneo, applies closely to these specimens, making slight allowances for differences in the state of preservation of the examples examined.

# (6) Otostigmus angusticeps, sp. n.

Colour a uniform green, head slightly rufescent: anal legs banded with darker green.

Head oval, elongate, rather coarsely but sparsely punctured antennae with 19 segments, of which the basal two or three are naked.

Precoxal plates of maxillipedes armed with 3-3 teeth, the two inner fused, the outer isolated.

Tergites smooth, punctured, not spicular, and not noticeably wrinkled, from the 5th bisulcate, from the 9th marginate.

Sternites also smooth, strongly and completely bisulcate, with an anterior and posterior median impression.

Anal somite: tergite posteriorly impressed: sternite broad: pleurae elongate, with two apical spines and one external spine near the base of the process.

Legs moderately long, femur armed with 11 strong spines arranged in four rows 3, 3, 2, 3: tarsus unspined. Protarsal segment of the remaining legs spined.

Total length 41 mm.: of anal leg 11, of antennae 12.

Loc. New Britain.

Differs from the preceding species in the smoothness of the dorsal and ventral surface, the completeness of the sulci on the sterna, the fewer spines and absence of protarsal spur on the anal legs.

# GENUS. Ethmostigmus, Poc.

# (7) Ethmostigmus platycephalus (Newport).

Heterostoma platycephalus, Newp. Trans. Linn. Soc. XIX., p. 415 (1845).

Loc. New Britain. Previously recorded from Halmahera, New Guinea, Tahiti, Duke of York Island, etc.

# (8) Ethmostigmus granulosus, sp. n.

Colour a tolerably uniform olive brown, with metallic reflection; lower surface olive yellow, antennae olive green at the base, distally covered with fulvous pubescence; maxillipedes and anal pleurae castaneous; legs olive green with pale yellowish basal and tarsal segment.

Antennae with 20 segments, whereof the basal 3-4 are naked.

Head and tergal plates finely punctured; the middle and posterior tergal plates very finely but not very closely granular, the granulation thicker at the posterior end of the body than at the anterior end; tergal plates from the 5th bisulcate, from the 6th marginate: sternal plates very obsoletely bisulcate.

Anal pleurae long and slender, surpassing the middle of the femur and as long as the femur of the anal leg, armed with 1 lateral spine; 2 larger adjacent apical spines, above which there are usually 2, and below sometimes 1 smaller spine.

Anal sternite narrowed and emarginate posteriorly; its posterior width less than its length and only a little more than half its basal width.

Anal legs longish and slender, the femur nearly four times as long as broad, armed with only 8 spines, including the apical process, arranged from above downwards as follows: 3, 2, 1, 2; protarsus unspined. Protarsus of pre-anal leg and of all in front of it with a single spur.

Measurements in millimetres. Total length of body and head 78, of antennae 22, of anal leg 24, width of body 8, of head 6, of anal tergite 5.

Loc. New Britain. Two examples.

This species differs from previously described forms in the fine granulation of its tergal plates. Apart from this feature it may be recognised from the preceding species by having only 8 spines on the anal legs.

Dr Willey also obtained an example apparently referable to this species from Narowol, in the Solomon Islands, and the British Museum has others from the Duke of York Island, which Mr Butler confounded with specimens of *E. platycephalus*, describing the two as *Heterostoma brownii*. The type of *brownii*, however, seems to be cospecific with that of *H. platycephalus*.

ORDER. GEOPHILOMORPHA.

FAMILY. DICELLOPHILIDAE, Cook.

Genus. Mecistocephalus, Newport<sup>1</sup>.

Proc. Zool. Soc. 1842, p. 178.

(9) Mecistocephalus punctifrons (Newport), loc. cit.

Loc. New Britain.

### (10) Mecistocephalus lifuensis, sp. n.

Colour yellow, head and maxillipedes castaneous.

Head-plate sparsely punctured, a few larger punctures amongst the smaller; two posterior grooves prominent; basal plate, maxillipedes and 1st tergite also sparsely punctured. Each maxillipede armed internally with 5 tubercular teeth.

Sterna, except the posterior, marked with median groove, which at the anterior end of the body is Y-shaped. Sternite of anal segment broad at the base, triangularly pointed posteriorly.

Pleurae moderately inflated, furnished with only about 20 large scattered pores. 51 pairs of legs. Length 34 mm.

Loc. Lifu (Loyalty Islands).

<sup>&</sup>lt;sup>1</sup> This genus of Newport's was primarily based upon the following species: ferrugineus, maxillaris, punctifrons and guildingii. The first of these, ferrugineus, was subsequently, that is to say, in 1847, taken out as the type of Pachymerium, and carries with it the second species, maxillaris. This left the two following species punctifrons and guildingii to represent Mecistocephalus, and the former was practically selected as the type by Wood (1869), and Meinert (1870). Thus by the process of elimination punctifrons will stand as the type of Mecistocephalus, of which Lamnonyx of Cook will be by this method a synonym.

In possessing 51 pairs of legs this species resembles *L. gigas* of Haase (Abh. Mus. Dresden, No. 5, p. 105, Pl. vi. fig. 111) recorded from New Guinea, but apart from its much smaller size, *gigas* attaining a length of 105 mm., *L. lifuensis* certainly differs in having the anal pleurae but little inflated and the pores large, few in number and not close-set. Haase describes these organs in *gigas* as follows:—"pleurae posticae valde efflatue, rotundatae, poris perminutis plurimis perforatae." Mr Cook, it may be added, has recently established the genus Megethmus for M. microporus of Haase (Proc. U. S. Nat. Mus. XVIII., p. 74, 1896).

FAMILY. GONIBREGMATIDAE, Cook.

Proc. U. S. Nat. Mus. xvIII., p. 16, 1895.

GENUS. Gonibregmatus, Newport.

Newport, Proc. Zool. Soc., 1842, p. 181; Linn. Trans. XIX., p. 434, 1845. Pocock, Max Weber's Zool. Ergebnisse, etc., Vol. III. pt. 2, pp. 317-319, 1894.

Sub-frontal plate of head hairy; produced downwards into a triangularly pointed prominence which supports the labrum at its apex; labrum consisting of a small semicircular plate of which the whole of the free margin is pectinate; that is to say, armed with fine, close-set spinules. (Figs.  $1\,c-1\,d$ .) Laminae fulcientes irregularly hammer-shaped, with a slender posterior process which nearly meets its fellow of the opposite side in the middle line. Closely pressed against the laminae fulcientes and lying in the hollow formed by the labral process in front lie the mandibles. Each of these is composed of two branches, an outer and an inner; the former are in front of the latter, broad at the base, pointed at the apex, with the outer margin bristly, the inner or biting margin pectinate; the inner and posterior branches of the mandibles meet in the middle line throughout their length, though apparently without actual fusion, forming together a broadly triangular plate, the distal portion of which is membranous. (Figs.  $1\,e-1\,g$ .)

Maxillae forming a plate, the free part of which is composed of a pair of rounded unsegmented plate-like, hairy lobes. (Fig. 1 h.)

Maxillipedes of 1st pair robust, coxa produced posteriorly, the rest of the segments thickly hairy or bristly, the claw strong.

Maxillipedes of 2nd pair with coxal plate twice as wide as long, the rest of the appendage slightly overlapping the head at the sides, with long, powerful claws. (Fig. 1c.)

Head-plate about as long as wide, with very distinct and large frontal plate.

Antennae broad at the base, distally parallel-sided, segments more or less moniliform. Prebasal plate small, transversely lanceolate; basal plate wider than head.

Tergal plates with a pair of impressions, one at each side, rugose mesially.

 $Sternal\ plates$  with the pores apparently arranged in irregular transverse areas.

As many as five *pleural sclerites* above the stigmatiferous sclerite; *stigmata* vertically linear.

Anal pleurae inflated, finely porous, encroaching upon the antepenultimate segment; anal tergite narrow, sternite wider than long; no anal pores. Anal appendages of male two segmented; legs of male not inflated. (Figs. 1 a—1 b.)

This interesting genus was previously only known from a couple of specimens, each the representative of a particular species. Consequently up to the present time no detailed information respecting the mouth-parts was forthcoming.

Dr Willey, however, was fortunate enough to obtain several specimens of a third species in New Britain. I have therefore taken the opportunity to make the necessary dissection of the jaws and to supplement the diagnosis of the genus and family by describing them.

When establishing the family, Mr Cook, judging from the other structural features of *Gonibregmatus*, ventured to prophesy that the mouth-parts of this genus would prove to be peculiar. Examination has amply justified the prediction; for in the formation of its mandibles, which seem to retain a primitive bi-ramous character, *Gonibregmatus* stands alone in the class Chilopoda.

(11) Gonibregmatus anguinus, sp. n.

# Pl. VI, Fig. 1.

Colour a uniform yellowish brown, with a bright red transverse band on the head. Number of pairs of legs 129 ?, 115 %.

Length of ♀ up to 130 mm., of ♂ from 70-115 mm.

Loc. New Britain.

It is needless to describe this species in greater detail, since it appears to differ from the two previously established species of the genus in the characters set forth in the subjoined table:—

- (a) Prescutum of anal somite distinct, separated from the tergite behind it by a deep transverse groove; 161 pairs of legs in \( \cap \ldots \cdots \
- (b) Prescutum of anal somite either completely fused with the tergite or separated from it by a shallow suture; 129-131 pairs of legs in ♀.

When comparing G. cumingii and G. insularis on a previous occasion, I pointed out what at the time appeared to be two differential characters for cumingii, namely, the overlapping of the head-plate in front by the maxillipedes and the forward extension of the anal pleurae nearly to the posterior extremity of the fourth somite from the end. Both of these characters I now believe to be due to shrinking of the sclerites owing to drying.

w.

# FAMILY. EUCRATONYCHIDAE, nov.

Eucratonyx, gen. nov.

Pl. VI, Figs. 2-2 c.

Antennae broad at the base, attenuated apically.

Head covering maxillipedes, frontal plate distinct, suture weak; basal segment almost as wide as the head, but not covering the pleurae of the maxillipedes; prebasal plate either concealed by the head or appearing as a transversely linear sclerite.

Labrum not coalesced, undivided, appearing as a broad transverse plate the edge of which is sinuous, slightly convex at the sides, broadly and shallowly emarginate in the middle; armed with about thirty spinules, horny and close-set in the middle, transparent and directed inwards at the sides. (Fig. 2.)

Mandibles with the cutting edge toothed anteriorly (internally), pectinate posteriorly (externally) [apparently with only one pectinate and one dentate lamella]. (Fig. 2 a.)

Maxillae with external branch two-jointed; internal branch large and lobate. (Fig. 2b.)

Maxillipedes of 1st pair with their coxae united by a narrow bridge; claw strong and pectinate. Coxal plate of second maxillipedes about twice as wide as long; chitinous lines distinct.

Tergites strongly bisulcate. Sternites with pores arranged in an irregular posterior transverse series, a few scattered pores in the middle and fore part of the plates. Stigma-bearing sclerite in contact with tergite.

Anal pleurae moderately inflated, covered but not closely with fairly large pores; anal legs long, moderately thick, clawless.

Type, Eucratonyx meinerti (Poc.).

This species was described originally under the genus *Himantarium* (Journ. Linn. Soc. XXI., p. 289, pl. XXIV., fig. 1; also Ann. Mus. Genova, XXX., p. 42, 1891). It certainly, however, differs in many important characters from *H. gabrielis*, the type of the last-named genus. Nor am I able to bring it into line with any of the families of Geophilomorpha established by Mr Cook. I am consequently compelled to create a new family for its reception. Tested by Cook's analytical table of the families of this group the *Eucratonychidae* fall alongside the *Schendylidae* under section D, but the size of the head and basal plate as compared with the prehensors (2nd maxillipedes), the distribution of the sternal pores, etc., seem to prohibit such a reference.

# (12) Eucratonyx hamatus, sp. n.

### Pl. VI, Fig. 2c.

This species and E. meinerti may be distinguished as follows:

 CLASS. DIPLOPODA (Millipedes).

ORDER. POLYDESMOIDEA.

FAMILY. PLATYRRHACHIDAE.

GENUS. Acisternum, Silvestri.

Ann. Mus. Genova, xxxvi., p. 191, 1896.

(13) Acisternum flavisternus (Poc.).

Max Weber's Zool. Ergebnisse, III., pt. 2, p. 346, pl. xix., fig. 16. Loc. Tjibodas in Java.

The type specimens of this species were also obtained at Tiibodas.

In the synoptical table of the species of *Platyrrhachidae* taken by Max Weber (loc. cit., p. 344) it is stated with regard to this species, "Sternal areas unarmed." This is an error; for the sternal areas in the fore part of the body, that is from segments 3 to 10, are armed with tuberculiform spines. These are fairly strong on the 4th and 5th segments, but decrease in strength posteriorly and practically die out at the posterior end of the body. In *Acisternum monticola*, Poc., the type of the genus, the sternal spines persist to the posterior end of the body, though they become very small.

Parazodesmus, gen. nov.

Pl. VI, Figs. 3—3 b.

First tergite broadest across the middle, where it is furnished with a depressed rectangular keel.

Keel-bearing portion of the other segments covered, but not very closely, with rounded tuberculiform granules. Three rows of tubercles conspicuous, those of the anterior row as large as those of the posterior. Keels of medium size, depressed, anterior border basally shouldered and, like the posterior border, granular, lateral border tri- or quadritubercular, posterior angle produced but not spiniform.

Pore dorsal, behind the middle of the keel, and about equidistant from the lateral and posterior borders. Caudal process with margin convex and lightly notched. Sternal plate with two tubercles. Sterna granular, not spined. Copulatory feet with basal portion straight, apical portion strongly curved upwards towards the sternal process and giving off five slender processes, four long and one short.

This new genus is very nearly related in many of its features to Zodesmus, of which the only known species is tuberosus, Poc., from the Ki Islands (Ann. Mag. Nat. Hist. (6) XI., p. 131, pl. IX., figs. 3, 3b). The two may be distinguished as follows:—

- (a) Tubercles of anterior row smaller than those of the posterior; pores about one diameter from the lateral border and two from the posterior border of keels; caudal process more quadrate, with posterior border lightly convex; terminal portion of copulatory apparatus curved inwards, ending in three prongs.

  Zodesmus.

# (14) Parazodesmus verrucosus, sp. n.

Colour black or deep chocolate brown, keels flavous, cylindrical part of the segments pale above with a median dark spot; caudal process entirely dark; legs dark with flavous coxa and trochanter; sternal area dark, ventral portion of cylindrical half pale, antennae dark brown.

Antennae about equalling the width of the 1st tergite in length.

First tergite with its antero-lateral border evenly convex. Second tergite with its keels projecting below those of the 3rd, their lateral margins convex and five-tubercular. Anterior border of keels of the middle segments of the body transverse, anterior angle square, posterior angle acute, posterior border concave and directed slightly forward, posterior border of only the last four keels projecting backwards.

Hairs on legs clavate.

Male smaller than female; antennae longer than width of first tergite. The first two processes of the copulatory organ given off close together on the outer side of the terminal portion of the organ, the first (proximal) straight, directed backwards parallel to the axis of the foot, the second semicircularly curved inwards, upwards and backwards, the remaining three rising from a common base, the terminal pair long, subequal and subsimilar curved, the fifth one arising as a short backwardly directed process from the outer side of the base of the outer.

♀ length 36 mm., width 6 mm. Loc. Narowol, Solomon Islands.

Specifically this species may be distinguished from Zodesmus tuberosus as follows:—

#### FAMILY. STRONGYLOSOMATIDAE.

Aschistodesmus, gen. nov.

Pl. VI, Figs. 4-4c.

Resembling Strongylosoma, but differing in the entire absence of transverse sulcus upon the dorsum of the keel-bearing portion of the segments. Caudal process nearly parallel-sided, oblong, with truncate, lightly emarginate posterior border, tubercles not apparent. Sterna grooved longitudinally and transversely, with backwardly directed tuberculiform spines at the bases of the legs.

## (15) Aschistodesmus maculifer, sp. n.

Colour of head, antennae and segments entirely black, with a median yellow spot on the posterior portion of the dorsum of the keel-bearing portion of the segments; sterna and legs flavous.

Head smooth, antennae with segments from the second to the sixth gradually but only slightly increasing in length and thickness. Dorsum of all the segments smooth and polished; groove not sculptured. Keels conspicuous but small, with thickened margin, posterior angle produced, anterior strongly convex. Lateral surface smooth, without crest above the stigmatiferous tubercles. Legs with femur and tarsus the longest segments, femur about as long as patella and tibia taken together, and a little longer than the tarsus. Anal sternite with its median process a little surpassing the lateral tubercles.

Male with an undivided tuberculiform prominence upon the sternum of the 5th segment. Tarsi of legs of anterior nine segments with hairy pad. Copulatory organ (as in figure) broad and spatulate, its lower surface strongly convex from side to side, the external border deeply notched, a spiniform process behind the notch, internal border sinuate, the external surface anteriorly produced into a broad curved process bearing two slender nearly filiform processes; upper surface bearing two short hooked processes, one external, the other internal.

Measurements in millimetres. Total length 27 mm., width 3 mm.

Loc. New Britain.

#### ORDER. SPIROBOLOIDEA.

GENUS. Rhinocricus, Karsch.

(16) Rhinocricus cristovalensis, sp. n.

Pl. VI, Fig. 5.

Colour (in alcohol) a tolerably uniform olive brown, paler below, dorsum of segments marked by a median black longitudinal band with a yellow or red stripe on each side of it, the latter only about half the width of the former; these stripes traceable from about the 5th to the penultimate tergite; legs and antennae ochre yellow.

Female; head punctulate and striolate, frontal sulcus complete; eyes composed of 35 ocelli arranged in 6 transverse rows; antennae about as long as the head. Somites finely punctulate and striolate; transverse sulcus nearly obsolete dorsally, the area of the dorsum in front of the sulcus irregularly marked with transverse striae which inferiorly assume a longitudinal direction and are continuous with the normal longitudinal striae, which at the anterior end of the body extend nearly up to the pore; a faint longitudinal sulcus extending from the pore to the posterior margin. Scobina extending to about the 28th segment; the posterior border of the tergite just above it shallowly emarginate.

Anal tergite rectangularly produced, not surpassing the valves; valves lightly com-

pressed, with borders but little thickened; and sternite rectangularly produced.

Legs with a single seta on each segment except the tarsus, which is supplied with about six.

Male smaller and thinner than female; antennae longer than head; coxae of 3rd, 4th, and 5th legs a little produced; distal segments of these legs and of the following pair swollen beneath; tarsi of legs in anterior half of body padded. *Copulatory organ* as in figure. (Fig. 5.)

Number of segments 42-43.

length 51 mm., width 5.5 mm.; d length 43 mm., width 4.5 mm.

Loc. Maranta, San Cristoval.

# (17) Rhinocricus gazellensis, sp. n.

# Pl. VI, Fig. 6.

Colour a uniform black or olive brown throughout, except the anterior margin of the segments which shows as a pale band when the scobina is exposed.

Head smooth on labral portion, punctulate and striolate, sometimes rather coarsely wrinkled above; median sulcus strong above and below, weak in the middle. Eyes composed of above 46 ocelli arranged in seven transverse rows.

Somites smooth, polished, or at most finely punctulate dorsally; the transverse sulcus obsolete, scarcely traceable below the pore, represented above it merely by a shallow groove, the longitudinal striae extending up to or a little above the pore. Scobina traceable to about the 38th segment; posterior border of segments not bisinuate, furnished with a series of larger and smaller short, spaced, squamiform, clavate pectinate hairs. Anal somite small; tergite rectangularly produced, transversely impressed; valves posteriorly prominent, a little compressed towards the margin; sternite semicircular.

Male; legs of third pair with coxae and succeeding two segments produced; coxae of fourth also a little produced; tarsus of legs in anterior portion of body padded. Copulatory apparatus like that of *R. cristovalensis*, but the median process of the anterior sclerite is shorter and the process of the anterior lateral sclerite longer.

Number of segments 49-50.

Length of 2 77 mm., width 6 mm.

Loc. Gazelle Peninsula, New Britain.

## (18) Rhinocricus biincisus, sp. n.

? Colour olive black, the posterior rim of the segments pale, and the entire posterior portion reddish laterally; antennae and legs reddish yellow.

Transverse groove obsolete above the pore on all the segments except the anterior eight. Scobina large, the border of the tergite above it, distinctly sinuate.

Anal valves not prominent.

Number of segments 54.

Length 80 mm., width 7 mm.

Loc. Gazelle Peninsula, New Britain. A single ?.

The three species of Rhinocricus here described may be distinguished by the following table:—

- (b) Back without longitudinal bands and without transverse striae.

  - (b') Anal valves scarcely at all produced beyond the level of the tergite; scobina large; tergites noticeably bisinuate; legs and antennae reddish yellow......biincisus.

### GENUS. Spirobolus, Brandt.

### (19) Spirobolus carneipes, sp. n.

? Colour (in alcohol) a nearly uniform pale olive green, posterior border of segments with a narrow yellow band in front of which there is a darker stripe; anal segment olive black; legs clear reddish pink.

Head and segments densely punctulate throughout; transverse sulcus obsolete dorsally but traceable above the pore; pores small, apparently situated upon the sulcus.

Number of segments 44.

Length about 50 mm.; width 6 mm.

Loc. Isle of Pines.

This species has not been described at any great length on account of the closeness of its resemblance to S. caledonicus, Pocock (Ann. Mag. Nat. Hist. (6), XI., p. 253, 1893), from New Caledonia. The latter, however, has the legs entirely black and the head and segments smooth and polished. The two following species from New Caledonia no

doubt also fall into the genus Spirobolus as now restricted, namely, S. insulanus and S. albidicollis, Porat (Ann. Soc. Ent. Belg. XXXII., pp. 251–253, 1888), and both are evidently related to S. carneipes and S. caledonicus. The four species, however, seem to be separable by the following features:—

- (a) Segments not transversely banded, usually marked dorsally with a pair of red or yellow longitudinal stripes; legs pale. ......insulanus.
- (b) Segments transversely banded, without longitudinal stripes.

  - (b') Segments coriaceous or rugose.

S. detornatus, Karsch. (Zeits. Naturwiss. 54, p. 57, 1881), from Viti Levu, probably also belongs to this section. If so it will apparently differ from those species enumerated above in having the face divided by a deep sulcus and thickly marked laterally with oblique striae.

# GENUS. Trigoniulus.

### (20) Trigoniulus pulcherrimus, sp. n.

Colour (in alcohol); dorsum of segments occupied by a broad blood-red band divided in the middle line by a narrow black stripe, sides of the segments occupied by a broad black stripe; lower portion of segments also blood-red; first to gite and anal somite black; lower half of head pale, upper half black; antennae palely fuscous; legs entirely pale yellow.

Head and first tergite smooth; the rest of the segments with their posterior portion elevated and smooth or nearly smooth dorsally, striate laterally and in eriorly but not more than half-way up to the pore; the groove separating the anterior and posterior parts of the segments marked dorsally from pore to pore with a series of subcircular impressions; below the pore on each side the groove is impressed with the ends of the striae, which pass backwards on to the anterior portion of the tergites.

Pore situated upon or perhaps a little behind the groove. Anal tergite forming a blunt obtusely-angled point not surpassing the valves; valves lightly compressed; sternite with posterior border transverse.

Number of segments 46.

Length 30 mm., width 2.8 mm.

Loc. New Britain.

This species is very noticeable for its bright black and blood-red colouring.

#### ORDER, COLOBOGNATHA.

### GENUS. Bdellotus, Cook.

### (21) Bdellotus bivittatus, sp. n.

Head, antennae and first segment black; the rest of the segments black and polished, but marked dorso-laterally with two parallel white bands extending from the anterior to the posterior end of the body; the median dorsal black band about as wide as the lateral white bands; margins of tergites below the pores narrowly white; anal somite black; legs infuscate.

Number of segments 65.

Length 11 mm., width 8 mm.

Loc. Lifu, Loyalty Islands.

In its banded coloration the species calls to mind *Bdellotus formosus*<sup>1</sup> (Pocock), the type of the genus *Bdellotus*, from Java; but the latter has a single median dorsal white line and the first and last tergites are also white, whereas *B. bivittatus* has a median dorsal black band and the first and last tergites black.

#### EXPLANATION OF PLATE VI.

| 1 a. | 3.7 | 17 | 11 | last segment of d from above to show persisten    |
|------|-----|----|----|---|
|      |     |    |    | of suture (a), between the anal tergite (b), a    |
|      |     |    |    | the prescutum (c).                                |
| 1 b. | ,,  | ,, | ,, | last segment of of from below showing biarticular |
|      |     |    |    | genital appendages (a).                           |
| 1 c. | ,,  | ,, | 27 | labrum.   |
| 1 d. | ,,  | ,, | 17 | dentate margin of labrum.                         |
| l e. | ,,  | ,, | 11 | mandibles from behind showing outer branches      |
|      |     |    |    | and inner branches forming labial plate or lov    |
|      |     |    |    | lip(b).   |
| 1 f. | ,,  | 71 | ,, | left mandible from the front; outer branch        |
|      |     |    |    | with pectinate edge and labium $(b)$ .            |
| 1 g. | *1  | ,, | ,, | enlargement of portion of pectination.            |
| 1 h. | 22  | ,, | ,, | maxillary lobes of left side from the front.      |
| 1 i. | ,,  | ,, | ,, | maxillary lobes and maxillipede of left side fr   |
|      | • • |    |    | below (behind).                                   |

Fig. 2. Eucratonyx meinerti (Poc.) labrum.

2 a. ,, right mandible from below (behind).

2 b. ", maxillae and maxillipede of right side from below (behind).

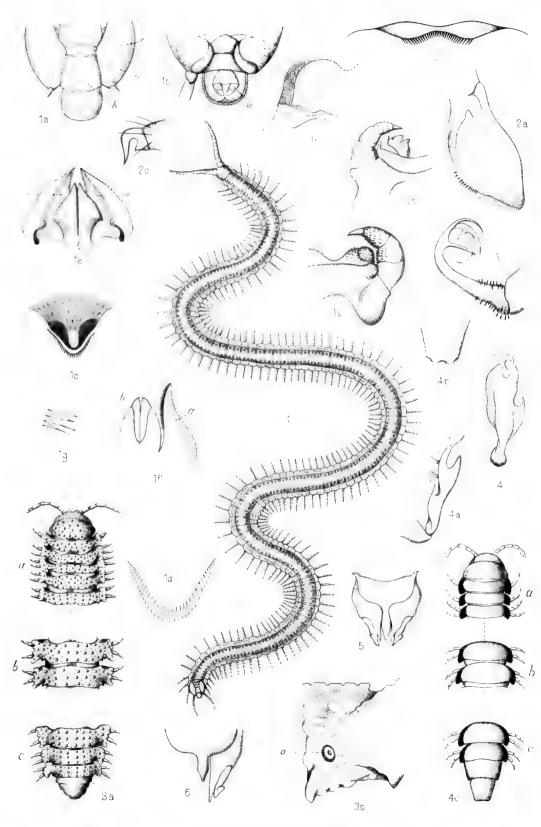
2 c. , hamatus sp. n. claw of one of the anterior legs.

<sup>&</sup>lt;sup>1</sup> Max Weber's Zool. Ergebnisse, III. pt. 2, p. 338, pl. xx. Fig. 5, 1894.

| Fig. | 3.   | Parazo desmus                           | verrucosus,   | gen. | et sp. | n.   | copulatory foot, external view.  |
|------|------|---|---------------|------|--------|------|--|
|      | 3 a. | >>                                      | 31            | 23   | "      |      | dorsal side of anterior end of body (a), of two median segments (b), of posterior end (c). |
|      | 3 b. | > 27                                    | >>            | "    | "      |      | upper side of left keel of segment 13 to she marginal armature and position of pore (a     |
| Fig. | 4.   | Aschistodesmus                          | maculifer,    | gen. | et sp. | n.   | left copulatory foot from below.   |
|      | 4 a. | ***                                     | ,,            | 77   | 19     |      | right copulatory foot from the outside.  |
|      | 4 b. | • | 13            | 2.2  | ,,     |      | caudal process.  |
|      | 4 c. | "                                       | 12            | "    | 23     |      | dorsal side of anterior end of body (a), of two median segments (b), of posterior end (c). |
| Fig  | 5    | Rhinocricus co                          | mietowalemeie | cm   | n cont | ılaí | apparatus (antorior asport)  |

Fig. 5. Rhinocricus cristovalensis, sp. n. copulatory apparatus (anterior aspect).

Fig. 6. Rhinocricus gazellensis, sp. n. copulatory apparatus (anterior aspect, portion of right half omitted).



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PUCUCA, MYRIAPUDA

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# ACCOUNT OF THE PHASMIDAE, WITH NOTES ON THE EGGS.

By D. SHARP, M.A., F.R.S.

With Plates VII—IX.

The specimens of this family of Orthoptera brought back by Dr Willey represent upwards of twenty species. Some of the species are represented only by individuals that are not full-grown, and I find that it is not desirable to deal with these, as we at present know but little of the post-embryonic development, so that it is difficult to determine what relations of colour, form and wing-development the young may bear to the adult. In the case of Eurycantha horrida I have identified the young with some probability of accuracy, and we have therefore figured some stages of the development. From what we find in the case of this species we may conclude that great changes in the external characters occur in the course of the development. Even when the difference between the sexes is very great in the adult state it is difficult if not impossible to distinguish the sexes in the young by external signs. Hence it is not at present desirable to describe and name new species from specimens that are not adult.

The species brought back from New Britain and Lifu in the adult state are six in number from Lifu, and eleven from New Britain. The Insect-fauna of these islands has not hitherto been the subject of any important study, and our knowledge of that of New Guinea is only small, so that it is scarcely a matter for surprise that a large proportion of the species—14 of the 17—appears to be unknown. Dr Willey was necessarily limited in his activity to a few spots on the coasts of the islands, and we may therefore conclude that many more species of these curious insects are existent in the two islands in question.

Under these circumstances it is not worth while to attempt any conclusions as to the geographical distribution. I may however remark that 53 species of Phasmidae are now known from Australia¹ and that they appear to have but little close

relation with those procured by Dr Willey; and it seems probable that a closer relationship with those of the islands to the West may be established. I may also remark that a great many of the Phasmidae recorded in the older works on entomology are said to come from Amboyna. I think this locality should not, without confirmation, be adopted as the real habitat of the species, as I doubt whether we can conclude more than that the ships bringing the specimens to Europe traded with that port. The uncertainty as to these old records will I fear delay any satisfactory conclusion as to the distribution of Malayan Phasmidae, at least until the Ceram and Amboyna fauna has been thoroughly investigated.

The young of Eurycantha. The adults of this genus are extremely remarkable; the number of spines on the body and the enormous size and curious armature of the hind legs of the male being especially conspicuous (Pl. VIII, Fig. 9). Dr Willey brought back a series of specimens in various pre-adult stages which I at first thought must represent more than one species, but which after comparison I believe to be stages in the growth, or instars, of E. horrida. Although probably no quite newlyhatched specimen is present, yet it is clear that most of the conspicuous characters of the species are acquired during the post-embryonic growth; almost the only resemblance between the youngest specimen and the adults are that both are broader and shorter than is usual in Phasmidae. The number of segments in the antennae is of great importance in the classification of the family; our series of E. horrida indicates a remarkable change in this feature during life. The youngest specimen we have has only nine segments on the antenna, whereas the adult has upwards of forty2. Nevertheless in the young the antennae are proportionally rather longer than in the adult, so that we have present the phenomenon of a great increase in number of segments, accompanied by an arrest of growth in comparison with other parts. Although our series is not sufficiently good to enable me to state with certainty the manner in which the change occurs, it would seem to be due to many of the segments of the young antenna dividing at once into a considerable number-about six-of smaller segments (Pl. VIII, Fig. 8).

The median segment of Phasmidae. It is commonly stated that the third thoracic segment in Phasmidae is formed by the union of the first abdominal segment with the metathorax. This view is stated by Brunner v. Wattenwyl<sup>3</sup>, and is adopted by Heymons<sup>4</sup>. The adult insect so far as its structure goes does not exhibit positive evidence in support of this view so far as the sternum is concerned. On looking at the metasternum it is easy to imagine that one can detect in it a sufficiently complex structure to justify the view above alluded to; but on comparing it with the mesosternum exactly the same parts seem to be also present there (Fig. 10). As there can be no question of an abdominal sternite being added to the mesothorax, the view that one is added to the metathorax should be confirmed by observation of the development.

<sup>&</sup>lt;sup>1</sup> For definition of this term refer to Cambridge Nat. Hist. v. p. 158.

<sup>&</sup>lt;sup>2</sup> Only one antenna of the adults is intact, and this has 49 segments.

<sup>&</sup>lt;sup>3</sup> Brunner v. Wattenwyl, Morph. Bed. Segm. Orthopt. Wien, 1876.

<sup>&</sup>lt;sup>4</sup> Heymons, SB. Ak. Berlin, 1897, p. 367.

The ovipositor and female genital appendages. The genital structures in Phasmidae have been too much neglected by entomologists: they have been avoided for the purposes of distinction of species, and their morphology has scarcely been inaugurated. The structures in the male are remarkable for their simplicity, the intromittent organ of the male being apparently a crumpled sac with five or six more or less vaguely defined sclerites in it. In the female the genital appendages are of great importance for distinguishing the species. The two species, Anchiale stolli and A. confusa, much resemble one another externally and appear to have been confounded by entomologists for upwards of a century; yet the female genital appendages distinguish the two satisfactorily, and the distinction is placed beyond doubt by a comparison of the eggs of the two forms. The ovipositor in certain other forms of Orthoptera -Locustidae and Gryllidae-has been shown to be formed by six gonapophyses, which appear as separate parts in the early stages of the post-embryonic development and subsequently become intimately combined to form the long, projecting ovipositor. Of these six gonapophyses four, according to Dewitz<sup>1</sup>, are appendages of the ninth segment and are really only a single pair secondarily divided; the other two are appendages of the eighth segment. In the female Phasmidae, six appendages are frequently present but they are never combined to form an organ for the deposition of the egg; they remain isolated finger-like processes (occasionally becoming so elongate as to be whip-like), and a part of their functions seems to be to hold the egg in the peculiar external uterus in which it remains till the female releases it, or till it is pushed out by the descent of another egg from the ovaries (Pl. IX, Fig. 16). These uncombined appendages appear to be homologous with the gonapophyses of the Locustidae as studied by Dewitz. One pair, the inferior, is separate and is anterior to the others in its attachment to the body. If we use Brunner's enumeration of the ventral sternites this pair of appendages belongs to the eighth segment, the ventral plate of which is prolonged to cover the genital appendages and to support the egg. The other two pairs are placed farther back and are merely prolongations of a large ninth abdominal sternite (Pl. IX, Fig. 25 c), as is well shown in the figure of the parts of an immature female of the genus Myronides (Fig. 26 b). The tenth sternite is very large, and is more or less deeply divided at the tip.

The male genitalia are very little known. Owing to the fact that so little material for study is available in the European fauna, nothing appears to have been published as to the organs of copulation. I have examined them in a very decayed male individual of Anchiale confusa, and find them to be remarkable from the existence of a very large sac which is covered by the pouch or receptacle formed by the ninth ventral plate; this membranous sac is formed by the ventral wall of the body, and when distended is found to consist of two imperfect pouches, portions of which are thickened and chitinised so as to form sclerites. Five or six of these indurated parts exist; they are quite asymmetric, and no two of them are at all similar; some of them are secondary projections from the wall of the sac, while others do not project at all. The hinder margin and the free angles of the tenth dorsal abdominal plate are also armed

<sup>&</sup>lt;sup>1</sup> Dewitz, Zeitschr. wiss. Zool. xxv. 1875, p. 174.

with teeth and tubercles in various species, and these apparently afford good specific characters (Pl. IX, Figs. 18, 19).

The egg. A correct account of the structure of the eggs of two or three species of Phasmidae has been given by Leuckart 1. As his account includes no reference to the incomplete egg or the mode of its growth the following observations may have some value. Phasmidae are insects of extreme interest; they appear to be the nearest living representatives of an Insect-fauna that was predominant in the carboniferous epoch; they exhibit an astonishing variety of grotesque forms, looking as if they were constructed of vegetable matter (so that some of them are called walking-leaves, others stick-insects) and they attain a size that is much above that of insects generally. They are exclusively vegetarian in diet, and are amongst the most inactive of insects. The climax of their peculiarities is found in the extremely perfect structure of their eggs and the resemblance of these eggs to seeds. The egg of a Phasmid has not only a general resemblance in size, shape, colour and external texture to a seed, but the anatomical characters of certain seeds are reproduced on the external surface, there being a hilar area, a hilar scar, and a capitulum corresponding to the micropylar caruncle of such seeds as those of the Castor-oil plant (Ricinus communis). The hilar area on the inner face of the capsule is, in shape, like the embryo of a plant (Pl. IX, Fig. 28). Moreover naturalists who have examined these eggs declare that the minute structures of this curious egg-capsule cannot be distinguished histologically from plant-structures. I think these resemblances, in the eggs I have examined, have no bionomic importance for the species. We have figured and described several of the eggs brought back by Dr Willey, and I have also added descriptions of two or three other interesting eggs obtained elsewhere.

In the examination of these eggs I have received much kind assistance from Dr Willey, and I think it may be of interest to state a few points we have ascertained as to their structure and the mode of their formation. I have examined the ovaries in Eurycantha horrida and in Anchiale confusa from specimens of these species brought back by Dr Willey in spirit and in a specimen of Hermarchus pythonius brought from Rotuma by Mr J. Stanley Gardiner. As these ovaries contain eggs in various stages of development it is possible to form an idea as to their mode of growth that may to some extent approximate to what actually occurs.

The capsule proper of the egg, or outer shell, is called chorion by Leuckart (who distinguishes an exochorion and an inner layer or endochorion); inside the chorion there is an inner membrane, the vitelline membrane or oolemn. The other important parts are the operculum, capitulum and micropylar area. All the parts of the egg are to the least detail formed in the ovarian tube. The operculum is present as a distinct part from a very early date, and so is the capitulum in those eggs in which it exists. When the egg is about half-grown the future exochorion forms merely a coat of quite soft matter which appears to appertain as much to the ovarian tube as to the egg; it can be removed with ease by a brush, and the egg is then found to consist of a yolk surrounded by two membranes similar in thickness. Of these the outer one subsequently becomes the inner wall of

<sup>&</sup>lt;sup>1</sup> In Müller's Arch. Anat. Physiol. 1855, pp. 214-220.

the capsule. In this membranous stage the micropylar area is quite distinct on the endochorion and exhibits a very similar shape to that seen in the completed egg.

The exochorion subsequently becomes hard and very perfectly attached to the endochorion. It differs in the egg of every species I have examined, being in some cases very thick (Leuckart says 1/6 of a millimetre in *Cyphocrania violascens*), but in other species it is quite thin (Gigantophasma). This secondary product is very vegetable-like.

The vitelline membrane is free from the endochorion except at the micropyle, where the two are firmly connected; another striking peculiarity of this membrane is that it is considerably thicker under the operculum than it is elsewhere.

Capitulum. This peculiar structure, placed on the middle of the operculum, is present in the eggs of the majority of species of Phasmidae but is entirely absent from others. It differs in every species, but when present is always a well-developed structure, and there are, so far as I know no forms in which it is present in an atrophied or rudimentary state; it is always either well developed or entirely absent. It consists of two parts, one of which is truly a part of the operculum; the capitulum itself is a less rigid body, superposed on the operculum and sometimes nearly concealing it (Pl. IX, Fig. 31). The part continuous with the operculum may form a stalk more or less elongate, and then projects to a greater or less extent into the soft body or capitulum proper, to which it forms a sort of core. The capitulum is present at an early stage of the formation of the egg, and if the half-grown egg of Anchiale confusa (Fig. 30) be looked at in the egg-tube it appears as if the capitulum is another less-grown egg attached to the larger egg. I think this will prove to be really the case and that the capitulum proper will be found to be the contents of another egg-chamber that have become subsidiary to the larger egg.

The species known to me in which the capitulum is entirely wanting are Brachyrtacus celatus, Eurycantha horrida, and Hermarchus pythonius (Figs. 32, 36, 41). I believe that the capitulum is also absent in the egg of Acanthodyta spiniventris, but this is not certain, as I speak only from my recollection of a single much damaged egg of which the operculum is now lost.

No function can be assigned to the capitulum in its formed state. It has, as was pointed out by Leuckart, no connection with the micropyle apparatus; it is not adapted to facilitate the admission of air to the egg, but must rather prevent such access. If it discharge any important function this is probably confined to a comparatively early period of the growth of the egg.

¿Operculum. This structure is present in all the known eggs of Phasmidae; it is a lid that fits very accurately to the truncate anterior extremity of the egg; its margin is surrounded by the margin of the capsule, and it is owing to the perfect fit between the two that the operculum retains its position. In the completed egg the operculum has no continuity with the capsule proper, neither have I been able to

¹ The egg of Cyphocrania violascens as figured by Leuckart, l. c. pl. x. figs. 19, 20, exhibits a small knob on the middle of the operculum. I think this is not a capitulum. The only mention of Cyphocrania violascens made by Westwood in his Catalogue of Phasmidae is as a synonym of Acrophylla violascens; this has been since referred by Stål to Tropidoderus, an insect now considered but distantly related to Cyphocrania. I do not know this insect or its egg.

demonstrate a continuity between the two parts at an earlier stage. The operculum it should be remembered is not seated on the chorion, but the latter is (apparently) quite absent from the anterior pole of the egg, where it is replaced functionally (as a covering and protecting body) by the operculum. In a comparatively early stage of the egg-growth, before there is any exochorion so that only the membranous endochorion is present, the operculum may be demonstrated as an independent structure placed on the volk, and enclosing a smaller body of volk. The egg itself may, at this stage, be entirely emptied of its yolk without affecting the opercular mass of yolk (Fig. 38). The exochorion of the operculum is formed subsequently, just as the exochorion of the capsule is formed subsequently, but there is no union between the two. The manner in which the operculum is formed is obscure; two methods may be suggested; 1, autotomy of the pole of the egg; 2, adhesion of the mass of matter from the adjacent nutrient chamber, to form as it were a very imperfect second egg. On this latter view the egg and operculum may be considered as the equivalent of an egg and a mass of matter added from another egg-chamber, and in that case when a capitulum is also present the egg would consist of egg-proper + opercular mass of nutrient matter + capitular mass of nutrient matter1.

The fact that the vitelline membrane is thicker about the opercular area where the chorion is absent suggests that the missing part of the latter may possibly be added to the former, and thus account for the thickness. But on the other hand it is quite probable that the extra thickness may arise in course of the process of autotomy, if that be the method by which the operculum is formed.

The egg of a Phasmid, provided as it is with a separate and perfectly fitting operculum, is a very remarkable object. Hitherto it has appeared to me very difficult to imagine how it could have been produced by a gradual process of evolution. From the imperfect study I have now made I think it probable that the Phasmid egg will be found to consist of an egg proper and of one or two imperfect eggs mechanically coadapted by pressure arising from the enormous distention of the egg-tube. It appears to me reasonable to suppose that it might have been thus produced in a gradual manner in the course of time.

The observations on the spirit specimens may be thus summarised:

- 1. The ovarian tube contains nutrient matter divided segmentally into separate masses, and the lower part of the tube is constricted so as to form chambers in each of which there is a mass of nutrient matter.
- 2. The mass of matter in the lower chamber grows enormously so as to cause extreme distension of the egg-tube, and the whole mass of matter in the chamber (or very nearly the whole) is found to be covered with two membranes (endochorion and oolemn), the outer one of which is deficient at one pole of the egg where the (as yet membranous) operculum is situate.
  - 3. The exochorion accumulates between the wall of the egg-tube and the outer

<sup>&</sup>lt;sup>1</sup> I think it probable that some other curious forms of Insect-eggs (e.g. those of Cynipidae and some Hemiptera Heteroptera) may prove to be compound eggs of this nature; that is to say, formed by the combination of the more or less separate growths of more than one egg-chamber.

of the two egg-membranes and subsequently becomes perfectly adherent to the latter so that in the completed egg the two cannot be separated.

4. All the details of structure of the egg are completed in the chamber where the formation commenced.

I have arranged the genera in the order adopted by Brunner in his valuable "Revision du système des Orthoptères"."

#### ORTHOPTERA.

Family. Phasmidae.
Tribe. Lonchodides.
Genus. Myronides.

Myronides. Stål, Recensio Orthopterorum, III. Stockholm, 1875, p. 8.

This genus was established by Stål for two species from the Moluccas, and very little has since been added to it. In New Britain however the genus appears to be represented by numerous species. The chief character to distinguish it from Lonchodes is the longer median segment. Stål has not given any particulars as to the sexual distinctions, but I anticipate that the males and females are very different, so that direct observation will be required to match them. M. binodis is a very interesting form, as the peculiar nodes at the apex of the metanotum evidently represent wings in a rudimentary or vestigial condition (Pl. VII, Fig. 2).

# SECT. I. VERY SLENDER INSECTS [MALE ONLY KNOWN].

- (1) Myronides filum, n. sp. Pl. VII, Fig. 1.
- 3. Perangustus, olivaceo-testaceus, antennis fuscis, mox ante apicem albidis; capite anterius tuberculis duobus distantibus, acuminatis armato, posterius subquadrituberculato; metanoto posterius utrinque vix gibboso, processu minuto instructo.

Operculo subgenitali abdominis haud convexo, apice rotundato medio leviter emarginato; lamina subanali profunde canaliculato, cercis liberis, sat elongatis; lamina supra-anali profunde emarginata; processu apicali interne tuberculis acutis circiter 16—24 instructo.

Long. corp. 76 mm.; antenn. 53 mm.; cap. post antenn. 3 mm.; pronoti 3 mm.; mesonoti 19 mm.; metanoti 6 mm.; segm. med.  $4\frac{1}{2}$  mm.; abdominis 39 mm.; femor. ant. 24 mm.

Var. fusco-nigricans.

Loc. New Britain.

There are no tuberosities or asperities on the surface of the body, and the two teeth at the apex of each femur are very minute. The first joint of the antenna is straight-sided and rather narrow.

If I am right in considering the two dark specimens as the same species, it is possible that this insect is dimorphic in colour; there are at any rate no intermediates in our small series.

# (2) Myronides binodis, n. sp. Pl. VII, Fig. 2.

?. Perangustus, testaceus, antennis ad apicem pallidioribus; capite anterius mutico, vertice obsolete quadrituberculato; metanoto posterius utrinque gibboso.

Operculo subgenitali convexo, medio prominulo, apice late emarginato.

Although at first sight similar to *M. filum* this species is very easily distinguished by the absence of processes on the front of the head, by the binodose metathorax, by the different proportions of the metanotum and median segment, and the prominent male operculum. The curious short sacs attached to the metathoracic gibbosities clearly represent the wings, though they have the texture of the integument in general.

Long. corp. 76 mm.; antenn. 53 mm.; cap. post antenn. 3 mm.; pronoti vix 3 mm.; mesonoti 19 mm.; metanoti 8 mm.; segm. med.  $4\frac{1}{4}$  mm.; abdominis 38 mm.; fem. ant. 23 mm.

Loc. New Britain.

# SECT. II. BROADER INSECTS [FEMALE ONLY KNOWN].

# (3) Myronides bituber, n. sp.

\$\delta\$. Corpore granuloso, fusco-testaceo, pedibus testaceis fusco-variegatis, antennarum apice albido; capite processubus duobus acuminatis, magnis armato; abdomine carinato, carina anterius obsoletescente, segmento sexto medio bituberoso.

Long. corp. 120 mm.; antenn. 60 mm.; capitis (pone antenn. acetab.) 5 mm.; pronoti 5 mm.; mesonoti 26 mm.; metanoti  $9\frac{1}{2}$  mm.; segm. med.  $5\frac{1}{2}$  mm.; abdom. 59 mm.

Loc. New Britain. One specimen.

Although at first similar to the other species here described this may be readily distinguished by the pair of peculiar tuberosities on the dorsum of the sixth abdominal segment.

Egg (Pl. IX, Fig. 33): 3 mm. long; capsule covered with numerous large pores, and with a scanty coarse but slightly elevated reticulation; micropylar area not extending to the operculum, and moderately distant from the opposite pole, rather narrow; micropylar scar very obscure. Operculum bearing a black sessile capitulum, and surrounding this a slightly elevated ring. Described from eggs deposited by the female in New Britain while in Dr Willey's possession.

# (4) Myronides simplex, n. sp.

Q. Angustus, cylindricus testaceo-griseus, antennis pedibusque subvariegatis, illis ad apicem albidis, apice ipso minute fusco, articulo primo ovale; capite superne processubus duobus distantibus, mediocriter elevatis, acuminatis; tarsorum anticorum articulo primo superne alte carinato; abdomine segmento sexto dorsali in medio

utrinque tuberculo vix perspicuo armato: femoribus subtus versus apicem minute bidentatis.

Long. corporis 104 mm.; lat. corp. vix 5 mm. Long. antenn. 60 mm.; capitis post antenn. 5 mm.; pronoti  $4\frac{1}{2}$  mm.; meson. 25 mm.; metan. 8 mm.; segment. med.  $6\frac{1}{2}$  mm.; abdominis 55 mm.; femor. ant. 24 mm.

Loc. New Britain.

Readily distinguished from *M. bituber*, by the smaller processes on the head, and by the tuberosities on the abdomen being almost entirely absent. The male is unknown. The surface is uneven, the inequalities forming on the prothorax indefinite tubercles.

# (5) Myronides sordidus, n. sp.

Q. Robustus, griseo-testaceus, antennis mox ante apicem albidis, corpore superne sparsim irregulariter granuloso; capite anterius processubus duobus distantibus sat elongatis, acuminatis, apicibus versus antennas directis; antennarum articulo basale sat lato, margine interno curvato; tibiis anterioribus intus acute carinatis, carina versus basin altiore; lamina supra-anali acuminata, carinata.

Long. corp. 104 mm.; antenn. 62 mm.; tib. ant. 27 mm.; cap. post antenn. 4 mm.; pronot.  $4\frac{1}{2}$  mm.; mesonoti 27 mm.; met. 10 mm.; segm. med.  $5\frac{1}{2}$  mm.; abdom. 53 mm.

Loc. New Britain.

Only one individual of this species was obtained. It is closely allied to the typical species of the genus—M. pfeifferi—but is smaller, and the legs are somewhat differently formed. The two teeth on each femur are minute.

Egg (Pl. IX, Fig. 34): an egg taken from the ovipositor of the specimen after preservation for a year or more in spirit, much resembles that of *M. bituber* but with strongly-marked distinctions; the texture of the capsule is different; the capitulum is not sessile, but is elevated on a short stalk, and the ring surrounding it is strongly elevated and irregularly serrate (Fig. 34 a). The micropylar scar is linear and the micropylar orifice is exposed and surrounded only by a small obscure ring.

# (6) Myronides ramulus, n. sp. Pl. VII, Fig. 3.

2. Sordide testaceus, irregulariter fusco-subvittatus, parce, obsolete granuloso; capite mutico: abdomino segmento decimo margine posteriore utrinque biacuminato; lamina supra-anali acuminata; operculo compresso-carinato; appendices inferiores et mediani aequilonges, elongati.

Long. corp. 106 mm.; antenn. 52 mm.; capitis post antenn.  $4\frac{1}{2}$  mm.; pronoti 4 mm.; mesonoti 26 mm.; metan.  $10\frac{1}{2}$  mm.; segment. med. 5 mm.; abdominis 56 mm.

Var. fusco-subvariegato, haud discrete vittato.

Loc. New Britain.

In this species the granulation of the surface is more distinct on the metasternum. As it and *M. binodis* both have the head unarmed it is possible they may be the sexes of one species. There is no trace of the rudimentary wing-sacs in *M. ramulus*.

12 - 2

In addition to the type specimen and the variety, Dr Willey found a nymph evidently near the last ecdysis, being of about the full size. The stripes are very distinct in it.

#### GENUS. Brachyrtacus, n. g.

Q. Antennae elongatae, multiarticulatae, corpus inerme apterum, pedes simplices, segmentum medianum vix discretum, sat breve, metanoto multo brevius; abdomen in processu subacuminatum prolongatum; cerci minuti.

# J. Incog.

This genus very much resembles Hyrtacus Stäl, but has a shorter head and a longer median segment. Few Phasmids are so destitute of conspicuous characters. The elongate, terminal, ovipositor exists in but few genera and will aid those who have not access to an exponent of Hyrtacus in recognising this form.

In addition to the median segment there are only eight dorsal abdominal plates and the elongate terminal process. The latter structure is doubtless formed by the fusion of the ninth plate and the lamina supra-analis; in Eurycantha the two parts remain distinct.

The genus Hyrtacus is Australian, and only two species are referred to it as yet. Stål made the elongate head of *H. tuberculatus* one of the chief characters of the genus. *B. celatus* has a head of only the length of ordinary Lonchodides, and I have therefore been obliged to treat the New Britain insect as a distinct genus.

# (7) Brachyrtacus celatus, n. sp. Pl. VII, Fig. 4.

9. Pallide fuscus, lividus, inornatus; subtiliter punctatus; capite canaliculato.

Long. corp. 70 mm.; antenn. 47 mm.; capitis post antenn. 2 mm.; pronoti  $2\frac{3}{4}$  mm.; mesonoti  $16\frac{1}{2}$  mm.; metan.  $6\frac{1}{2}$  mm.; segm. med. 2 mm.; abdom. 40 mm. (lam. supraanalis cumque abdominis segm. ult. 9 mm.); femor. ant. 17 mm.

Loc. New Britain.

The three specimens found by Dr Willey are extremely similar. An immature nymph of the male sex renders it probable that the male will be found to closely resemble the female in size and form. The colour of this nymph is pale green.

Egg (Pl. IX, Fig. 32). The egg of this species is remarkable for its long slender form; at first sight it might be supposed to be the egg of a Locustid, but the operculum is quite definite and the micropylar area is well-marked; there is no capitulum. We have only one specimen, it has been damaged by fracture just across the micropylar scar so that the details of the structure are obscured.

### TRIBE. Clitumnides.

# GENUS. Eurycantha.

Eurycantha. Boisduval, Voy. de l'Astrolabe, Zool. Ent. p. 647.

The remarkable insects composing this genus appear to be peculiar to New Guinea and the neighbouring islands.

# (8) Eurycantha horrida. Pl. VIII, Fig. 9.

Eurycantha horrida. Boisd., Voy. de l'Astrolabe, Zool. pl. 10, f. 2. Westwood, Cat. Phasm. p. 63.

A fine series of this insect was procured by Dr Willey in New Britain. In the adult state it varies but little; the antennae are usually more or less deficient as to their terminal joints; the proper contingent appears to be about 48.

Several specimens that I believe to be young of this species were procured (Figs. 7, 8); if so, it appears to be variable in colour in early life; most of these young are similar in colour to the adults except that they are not quite so dark; two specimens are of a pallid stone-grey colour, maculated with darker fuscous marks. It is possible, however, that one or both of these specimens may be of another species; Kaup has described a second Eurycantha as occurring in New Guinea. The young specimens are in various stages of development, and they at any rate show that the armature of spines on the body and legs is developed gradually during the process of growth. The number of joints of the antennae is apparently the same throughout the later period of development, though the distinctness of their segmentation is less marked in the young, and in the very young there is a major segmentation into 7 or 8 joints, without any distinct segmentation of either of these into a larger number of joints (Fig. 7 a). The genital appendages of the female are also developed gradually, so that it is very difficult to distinguish the two sexes in the young.

Egg (Pl. IX, Fig. 41). Dr Willey kept specimens of this species alive and was able to observe that the eggs are dropped one at a time. On August 11th he noticed an egg in the ovipositor which was still in that position next day; on the 13th he found one egg was deposited: on Aug. 14th the same female had another egg ready for deposition, and this was still in situ the following day but was deposited on the 16th, and on the same day another egg was in the ovipositor and was deposited on the 17th: on the 18th the same specimen laid three eggs, and another on the 19th. The egg is large, 8 mm. long. It is of a grey colour, irregularly mottled with black and the whole surface of the capsule is covered with fine raised lines. The hilar area is broad and short, oval, the scar is broad and widely open in front. There is no trace of any capitulum on the operculum but the central area is slightly pinched together, and has a slightly different texture when highly magnified (Figs. 41 a, 41 b).

# Tribe. Acrophyllides. Genus. Acanthodyta, n. g.

Antennae breves, circiter 20-articulatae; thorax et abdomen spinosa; pedes mediocriter elongati, femoribus omnibus fere inermibus, marginibus superioribus et inferioribus omnium tantum minutissime spinulosis; tegmina nulla; alae utriusque sexus brevissimae. Segmentum medianum elongatum, metathorace longius. Maris cerci robusti. Feminae cerci minuti haud exserti, lamina supra-analis valde prolongata; segmentum dorsale ultimum sub-prolongatum.

This genus, tested by Brunner's Tables<sup>1</sup>, runs down to Acrophyllidae, Platycraniae, and may be placed next Arrhidaeus.

<sup>1 &</sup>quot;Revision du système des Orthoptères," op. cit.

# (9) Acanthodyta spiniventris, n. sp. Pl. VIII, Fig. 11 2.

Testacea, vel fusco-testacea; alis minimis, parte posteriore sanguineo-tincta; corpore lateraliter et superne spinoso; pedibus fere inermibus; capitis fronte bituberculata.

J. Cerci elongati, intus curvati.

Long. corp. 55 mm.; antenn. 17 mm.

Q. Lamina supra-anali ultra anum longe producta, acuminata; appendices anteroinferiores elongati, lineares, duri, ultra cercos extensi, apicem abdominis ventris attingentes; operculum subgenitale elongatum, apicem versus attenuatum, apice obtuso, lamina supraanali brevius; appendices mediani, elongati sublineares, cercos attingentes; appendices superiores nulli. Cerci breves sat lati, ad apices obtuse attenuati, margine externo ciliato-setoso.

Long. corp. 86 mm.; antenn. 20 mm.; capit. post antenn. 5 mm.; pronoti 5 mm.; mesonot. 18 mm.; metanot. (partis alas ferentis) 4 mm.; segm. med. (cumque parte posteriore metanoti haud discreta)  $5\frac{1}{2}$  mm.; abdominis 50 mm.; femor. ant. 29 mm.; tibia. ant. 38 mm.

Loc. Lifu.

Only one pair of the mature Insect was found. The male is much darker than the female in colour. A female nymph well advanced in growth has the spines of the upper surface represented only by minute acute tubercles.

Egg (Pl. IX, Fig. 40): an egg of this species was found in the ovipositor, but was damaged by extraction so that it has lost the operculum. The micropylar area extends the whole length of the egg and is at the farther extremity very distinctly divided into two processes that probably correspond with the attachment of membrane on the inner surface of the capsule.

# Genus. Graeffea.

Graeffea. Stål, Recensio Orthopterorum, III. 1875, p. 40.

The Insects of this genus appear to be peculiar to the Polynesian islands, where they are said to be sometimes very injurious by consuming the foliage of the foodplants of the human inhabitants.

# (10) Graeffea lifuensis, n. sp. Pl. IX, Fig. 21.

- Q. Testacea; prothorace subtiliter, irregulariter granuloso; alis brevibus, parte membranacea sanguinea.
- G. coccophagae peraffinis; cercis longioribus, lamina supra-anali medio longiore, acuminata; segmento mediano magis elongato.

Long. corp. 118 mm.; antenn. 23 mm.; fem. anter. 34 mm.; cap. post antenn. 6 mm.; pronoti 6 mm.; meson. 20 mm.; metan.  $5\frac{1}{2}$  mm.; segm. med. 6 mm.; abdom. 63 mm.; cerc.  $7\frac{1}{2}$  mm.; tegm. 7 mm.; alar. 14 mm.

The genital operculum is not convex, it is pointed and elongate, extending a little beyond the point of the lamina supra-analis. The superior and inferior genital appendages extend backwards to just the same point; the inferior are slender and filiform; the median and superior are short, as they merely form the divided extremities of a broad process; the median pair does not extend quite so far back as the lateral pairs.

Loc. Lifu: two specimens.

I have not seen the egg, but judging from the shape of the uterus I suppose it will prove to be elongate and slender. The uterus in this species is very different from what it is in Anchiale.

Only one or two species of this genus have been described, but judging from specimens in the British Museum there are several closely allied species, or forms, in the Polynesian islands. G. coccophaga was found in Rotuma in both sexes by Mr Stanley Gardiner, it is less elongate than G. lifuensis and has shorter legs. G. coccophaga is the species that is reputed to be at times very injurious, by consuming the foliage and soft parts of trees from the produce of which the human natives draw part of their sustenance.

# GENUS. Gigantophasma, n. g.

Antennae 30 articulatae, maris femoribus paulo longiores, feminae femoribus aequales. Maris, alae magnae; femina omnino aptera. Cerci maris sat magni, laminati, feminae maximi. Ocelli nulli. Segmentum medianum metanoto brevius, feminae segmento secundo abdominali toto, maris segmenti secundi dimidio, aequale. Maris metanotum in partes duas divisum. Segmenta abdominalia feminae lateraliter plus minusve lobodilatata. Pedes multidentati. Fem. operculum subgenitale ultra apicem abdominis extensum, lamina supra-analis nulla.

The position of this genus is uncertain. According to Brunner's tables, the male would come into Acrophyllidae (supposing that we consider the posterior division of the metanotum to be part of the median segment) and might be placed near Monandroptera. The female on the other hand would come into Clitumnidae near Medaura. The very large cerci induce me to place this curious form in Acrophyllidae, near Monandroptera, a genus about which little appears to be known. The female has a considerable general resemblance to Hermarchus pythonius, though differing greatly by the abnormal development of the cerci.

The male is of interest from the extremely definite division of the metanotum into two parts. The posterior of these is less distinct in some other forms, and in them is apparently counted as part of the median segment. Gigantophasma apparently shows clearly that the metanotum really consists of two parts. This is seen less clearly in various other Phasmidae.

# (11) Gigantophasma bicolor, n. sp. Pl. VII, Fig. 6 \(\frac{\pi}{2}\).

Fem. Fusco-viridis, superne a pronoti margine posteriore usque ad segmentum abdominis sextum viridis, segmentis late fusco-marginatis; abdominis segmentis 2—7 lateraliter plus minusve lobo-dilatatis, segmentis 8—10 parvis; femoribus posterioribus superne ad apicem lamina elevata ad apicem spinigera; tibiis rude spinosis.

Long. corp. ind. minor. 163 mm.; antenn. 43 mm.; cap. post antenn. 9 mm.; pronot. 8 mm.; mesonot. 30 mm.; metanot. 17 mm.; segm. med. 9 mm.; abdominis 88 mm.; cerci 9 mm.; femor. ant. 42 mm.

Lat. segm. med. 12 mm.; abdom. segm. 16 mm.; cerc. 6 mm. Long. corp. ind. major. 180 mm. Mas. Gracilis; testaceo-viridis, subfuscescens; abdomine segmentis 5 et 6, tenuiter lobo-dilatatis, lobis fuscescentibus; femoribus posterioribus spinis 5, elongatis, armatis.

Long. corp. 95 mm.; antenn. ultra 40 mm.; cap. post antenn.  $4\frac{1}{4}$  mm.; pronot. 4 mm.; mesonot. 15 mm.; metanoti partis alas ferentis  $5\frac{3}{4}$  mm.; pars poster. 4 mm. segm. med. 4 mm.; abdom. seg. secundi  $9\frac{1}{2}$  mm.; abdom. 58 mm.; cerc.  $4\frac{1}{2}$  mm.

Var. depictus. This species varies a good deal in colouration, and also in the form of the cerci, the length of the legs, and of the ovipositor, and even in the shape of the abdominal segments and their lateral expansions. In one individual the fuscous marks bear at the back of each thoracic and abdominal segment a pallid mark forming an inner margin to the fuscous marks; although I do not think this is a distinct species it may be well to give it a name.

Loc. Lifu.

Egg (Pl. IX, Fig. 35). The egg of G. bicolor is small in proportion to the size of the insect, being scarcely  $3\frac{3}{4}$  mill. long including the capitulum. It is less remarkable in structure than usual with Phasmid eggs. The surface of the capsule is densely and finely rugose. The lines limiting the micropylar area are not elevated, the micropylar scar is strongly elevated, forming a slightly curved transverse line, concealing the micropylar orifice. The capitulum is large without any trace of a stalk, and bearing a deep pit at the top. The shell of the egg is thin.

The egg in this species is variable like the insect itself: and it is possible that these forms may be "incipient species," but the material at my disposal is too small to allow me to form any decided opinion.

# (12) Gigantophasma pallipes, n. sp.

Fem. Viridi-testacea, antennis pedibusque pallidis; abdominis segmentis 2—7 lateraliter plus minusve lobo-dilatatis, segmentis 8—10 parvis: femoribus intermediis et posterioribus, tibiis posterioribus ad apicem, absque lamina elevata.

Long. corp. (cum ovipos.) 187 mm.; (cetera fere ut in G. bicolore).

Loc. Lifu: a single specimen.

Independently of the pale colour—which is perhaps of little importance as a specific character—this Insect differs from all the specimens of *G. bicolor* by the absence of the elevated laminae on the middle and posterior femora and tibiae, and by the longer basal joint of the posterior tarsi, the upper margin of which is not curvate. The ovipositor extends 12 mm. beyond the tip of the abdomen.

Dr Willey brought back a specimen which is probably the male of this species (Pl. VII, Fig. 5), as it has pallid legs and antennae: the small lateral lobes of the abdomen possess a metallic, golden, reflection, and the cerci are shorter and broader than they are in the male of *G. bicolor*, and the spines on the hind femora are more numerous (Pl. IX, Fig. 22).

[Hermarchus pythonius. Although this species was not obtained by Dr Willey, we figure the egg (Fig. 36) taken from the ovaries of a specimen brought by Mr Stanley Gardiner from the island of Rotuma. The sculpture of the capsule is remarkably coarse, and the operculum, which is destitute of a capitulum, has a very deep circular

depression round the central part. We also figure an egg-tube (Fig. 37) with the egg still incomplete though of large size: and the opercular pole of a less grown egg, in which the operculum can be distinguished with a mass of nutrient matter situate within it (Fig. 38).]

[Cyphocrania hanitschi, n. n. Dr Willey brought back eggs of a Phasmid which has been exhibited in a live state in the gardens and Museum at Singapore, as described in the report of Dr R. Hanitsch for 1897.

The Insect (probably undescribed) is allied to *C. goliath* Gray, and as the egg is remarkable for the large size of the capitulum we figure it, Pl. IX, Fig. 39. The micropyle is exposed and is readily perceived in consequence of the very slight elevation of the ring of the scar, Fig. 39 a.]

### GENUS. Anchiale.

Anchiale. Stål, Recensio Orthopterorum, III. 1875, p. 36.

Only one species of this genus appears at present to have been recognised, but it is very closely allied to the Malaysian Cyphocrania.

# (13) Anchiale stolli, n. n. Pl. IX, Fig. 16.

Elongata; mesothorace discrete tuberculato, tuberculis subacutis; cercis latis; alis fusco-brunneis, hyalino-maculatis,

Mas.; antennis elongatis (articulis 1—22 = 54 mm.); longe hirsutis, ocellis valde prominulis fere conjunctis; cercis ovalibus, angulo apicale per-obtuso; lamina supraanalis abrupte tectiformis, margine interno acute quinque dentato.

Long. corp. 106 mm.; pronot.  $4\frac{1}{2}$  mm.; mesonoti 16 mm.; metanoti  $8\frac{1}{2}$  mm.; segm. med.  $5\frac{1}{2}$  mm.; abdominis 68 mm.; cerci  $4\frac{1}{2}$  mm.; lat.  $2\frac{1}{2}$  mm.; tegm. long. 13 mm.; alae 60 mm.

Fem.; antennis brevibus (articulis 1—22=32 mm.), breviter pubescentibus; ocellis subobsoletis; cercis elongato-ovalibus, acuminatis; operculo obtuse acuminato ad apicem abdominis extenso, medio carinato; processubus genitalibus inferioribus elongatis, apicem laminae subanalis fere attingentibus; proc. medianis brevioribus, paulo ultra proc. superiores extensis; his latis, liberis, acuminatis.

Long. corp. 170 mm.; pronoti 9 mm.; mesonoti 25 mm.; metanoti 10 mm.; segm. med. 10 mm.; abdom. 100 mm.; cerci  $6\frac{1}{4}$  mm.; lat. 3 mm.; tegm. 30 mm.; alae 70 mm.

Loc. New Britain.

The species in the female sex is apparently dimorphic in colour, the tints being either those of young and green, or old and withered vegetation. I have only seen one individual of the male sex; it has six small teeth on the inflexed terminal portion of the last dorsal segment (Pl. IX, Fig. 19).

Egg (Fig. 27):  $4\frac{1}{2}$  mm. long,  $3\frac{1}{2}$  broad, of a slaty-grey colour, indefinitely mottled with paler grey, surface shining, a little irregular or uneven, not sculptured or porous. Micropylar area elongate, raised; micropylar scar large, almost horse-shoe shaped; capitulum pallid, rather small, placed on a short black base; operculum without sculpture, the middle part—in which the capitular stalk is placed—somewhat depressed after the fashion of a dish or plate.

This egg is remarkable on account of the absence of sculpture on the capsule; the stalk of the capitulum forms a conical process the terminal part of which projects into the pallid membranaceous top of the capitulum.

It is possible that Stoll's¹ figure of the male² and female³ of "Le spectre à aîles tachetées" may have been taken from this species. The locality he gives was, however, "Amboina," and the form of the cerci does not agree. His figure has been universally applied by synonymists to the following species, viz. A. confusa.

# (14) Anchiale confusa, n. n. Pl. IX, Fig. 17.

Cyphocrania maculata. Westwood, Cat. Orthopt. Phasmidae, p. 111 [nec Serville]. Fem. Elongata; mesothorace obsolete parceque granoso; cercis latis, alis fuscobrunneis, hvalino-maculatis.

Antennis brevibus, parce pubescentibus, ocellis subobsoletis; cercis brevibus, rotundatis; operculo minus obtuso, paulo ultra abdominis apicem extenso, medio carinato; processubus genitalibus inferioribus elongatis apicem laminae sub-analis attingentibus; processubus medianis inferioribus fere aequalibus; proc. superioribus elongatis, gracilibus.

Long. corp. 156 mm.; pronoti 7½ mm.; mesonoti 27 mm.; metanoti 8 mm.; segm. med. 9 mm.; abdom. 94 mm.; cerci 4 mm.; lat. 2¼ mm.; tegm. 27 mm.; alae 62 mm.

Loc. New Britain.

This species was met with by Dr Willey in two examples of the female sex, and an extremely decayed male. It is readily distinguished from A. stolli by the almost smooth thorax, and the more elongate, middle and superior (lateral) genital filaments; as well as by the rounded apices of the cerci. The male has three large, instead of six small, teeth on the inflexed margin of the last dorsal plate of the body (Pl. IX, Fig. 18).

This species is the *Cyphocrania maculata* of Westwood, according to specimens in the British Museum. Westwood was, however, in error in considering this to be the species designated by Stoll, Serville and others as *C. maculata*. Stoll did not at first give his species any name, but Serville and others took his figure as the type of their species, and if their assignment of a name on such grounds be attended to at all we must give a new name to Westwood's Insect. The name *Phasma necydaloides*, subsequently assigned by Stoll to his species, was then pre-occupied by Linnaeus.

The figure of *Platycrana necydaloides* in the *Voyage au Pôle sud* may possibly have been taken from a specimen of this or an allied species. It exhibits the thorax as entirely smooth. It is from the island of Warou.

Egg (Pl. IX, Fig. 29): 4½ mm. long, 3½ broad; slaty-black, densely covered with rugose sculpture. Micropylar area, narrow and compressed so as to be strongly raised, and to form a sort of band extending from the operculum to near the other pole of the egg: the micropylar scar coarse but not very distinct on account of the coarse, uneven, neighbouring sculpture, almost V-shaped. Capitulum small, pallid, placed on a short black stalk, obconic so as to be with the stalk almost funnel-shaped.

Stoll (Caspar), Afbeeldingen Spooken, etc. Amsterdam, 1787.
 Pl. IV, Fig. 11.
 Pl. III, Fig. 8.

Numerous eggs of A. stolli and A. confusa were deposited by specimens kept alive by Dr Willey. He noticed that when an egg is deposited another one immediately replaces it in the ovipositorial uterus. The generic resemblances between the eggs of A. stolli and A. confusa is very evident, but the specific distinctions are so strongly marked as to support the suggestion of Kaup that the eggs may possibly afford the best way of distinguishing closely-allied species of Phasmidae.

#### TRIBE. Phasmides.

# GENUS. Cacomorpha, n. g.

Corpus parum elongatum, maris alatum, feminae omnino apterum; pedibus parum elongatis, femoribus dilatatis fimbriatis, tibiis marginibus undulatis, tarsis margine interno sulcato. Antennis elongatis, 20-articulatis, articulis discretis; metathorace utrinque lobo singulo fimbriato, pendente (Fig. 23); metanoto breve; segmento mediano illo duplo longiore (in femina haud discreto); corpore subtus membranaceo, laevigato, metanoto utrinque loba libera ciliata; lamina subgenitali in utroque sexu breve, haud prominula.

This genus is evidently allied to Cotylosoma (C. Waterhouse, Ann. Nat. Hist. xv. 1895, p. 498) but that genus has tegmina and short wings in the female, and the side of the breast has five free lobes. Cacomorpha should no doubt be placed in Brunner's group Prisopi, but it is scarcely possible to assign a definite position in the present system of Phasmidae to these curious Insects. The antennae are much longer than the femora but possess only 20 joints. The tibiae are smooth beneath but have no apical area, though the Prisopi are placed by Brunner in the tribe Phasmidae, which is characterised by the possession of an apical area to the tibiae, and by being winged in both sexes. Prisopus is an American genus and has a short mesothorax, thus departing strongly from Cacomorpha. The sexual characters are peculiar, there being no genital appendages covered by the short, flat lamina subgenitalis of the female.

# (15) Cacomorpha aberrans, n. sp. Pl. VIII, Fig. 12 \cong2.

Corpore testaceo, fusco-variegato; subtus pallido, laevigato membranaceo; capite brevi inerme; mesonoto granulato; cercis sat elongatis sublineares.

3. Tegmina parva, alae magnae; abdomine sublineari, laevigato, tantum ad apicem rugoso.

Long. corp. 38 mm.; antenn. 20 mm.; capitis post antenn. 2 mm.; pronoti  $2\frac{1}{2}$  mm.; mesonoti  $5\frac{1}{2}$  mm.; metanoti  $2\frac{1}{4}$  mm.; segm. med. 5 mm.; abdominis 20 mm.; femor. ant 9 mm

9. Aptera, supra rugosa, abdomine lato.

Long. corp. 50 mm.; metanoti 2 mm.; segm. med. 5 mm.; abdominis 26 mm.; lat. abdominis 7 mm.

In the male the lamina supra-analis is not visible, in the female it forms a minute bifid process. The cerci are similar in the two sexes.

Loc. Lifu: one male, two females.

The specimens were brought to Dr Willey by natives, the species is certainly not aquatic, there being no water on Lifu except in wells. In all probability it lives closely appressed to the stems of bushes. Wood-Mason's idea that the lobes in Cotylosoma are tracheal gills seems to me to have no foundation whatever.

# TRIBE. Phylliides.

# GENUS. Phyllium auct.

Only two genera are recognised in this tribe, Phyllium and Chitoniscus Stäl, the latter being found in the Fiji islands. Dr Willey met with a species in Lifu which is exactly similar in appearance to *Chitoniscus feejeeanus*, but has the nervuration of Phyllium.

# (16) Phyllium brachysoma, n. sp. Pl. VIII, Fig. 13.

Q. Minor, viride; pedibus brevibus, femoribus parum dilatatis, anterioribus lobo interno parvo, intus rotundato, margine interno obscure tridenticulato.

Long. corp. 52 mm.; tegm. long. 32, lat.  $12\frac{1}{2}$  mm.; long. femor. ant.  $9\frac{1}{2}$  mm.; lobo interno long. 6, lat. 3 mm.

Loc. Lifu. Two female specimens.

This is the smallest Insect of the genus; it is in appearance allied to Chitoniscus feejeeanus, but is readily distinguished by the shorter form, and especially by the shorter legs, the front femora being in C. feejeeanum 11½ mm. long. There are only three distinct teeth on the lobe of the front femur, but near the apex, there are two other very minute denticles; there are no serrations between the denticles. The most marked difference between the two species is however to be found in the nervuration. In C. feejeeanus (Pl. VIII, Fig. 14) the radial vein diverges from the ulnar vein quite at the base, while in P. brachysoma the two run parallel and contiguous. As C. feejeeanum is known only by the very brief description given by Westwood (Proc. Ent. Soc. Lond. ser. 3, II. 1864, p. 17), we have figured the tegmen. P. brachysoma agrees fairly well with P. scythe in the nervuration, but it has the mesothorax short as in Chitoniscus, so that if Stål's genera are considered valid, P. brachysoma should form a third.

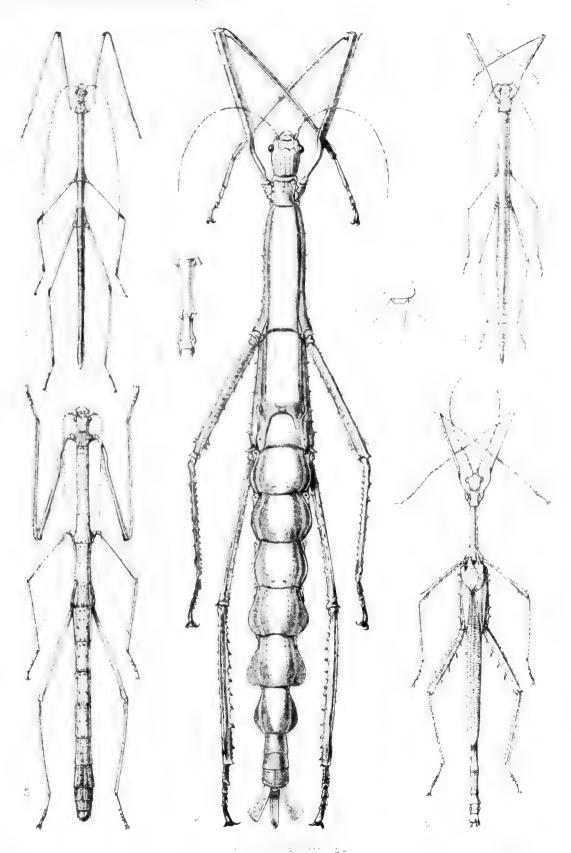
# (17) Phyllium, sp. Pl. VIII, Fig. 15.

Dr Willey brought a young nymph from New Britain which probably represents a new species of this interesting tribe, it being destitute of a lobe at the back of the front femur. *P.* (*Chitoniscus*) feejeeanus has been recorded as living in New Britain<sup>1</sup>, but I cannot identify this young individual as belonging to that species.

The sexes of Phyllium are in the adult state extremely different in form and in the condition of the wings, which are quite atrophied in the female but well developed in the male. The males are very rare and little is known as to the development of the sexual distinctions. In the nymph figured, the form is that of a female, but the hind-wings are as far advanced in development as the tegmina, so that I feel quite uncertain whether this nymph may be of the male or female sex.

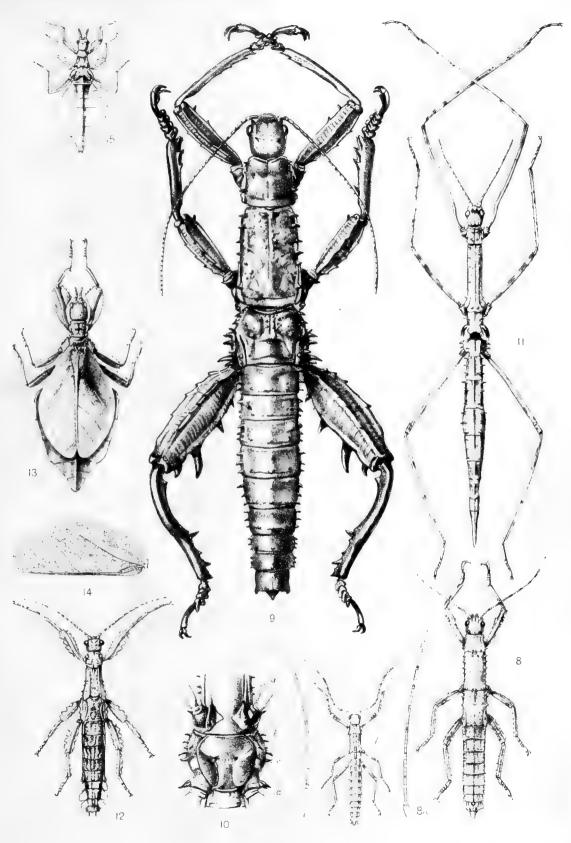
N.B. Phibalosoma novae-britanniae, Wood-Mason, Ann. Nat. Hist. (4) xx. 1877, p. 75, was not procured by Dr Willey.

<sup>&</sup>lt;sup>1</sup> Wood-Mason (Ann. Nat. Hist. xx. 1877, p. 75) described *P. novae-britanniae*, but subsequently (J. Asiat. Soc. Bengal, xxvi. pt 2, p. 351) considered this Insect to be *P. feejeeanum* Westw.



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SHARP. PHASMIDAE

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#### EXPLANATION OF PLATES VII—IX.

#### PLATE VII.

- Fig. 1. Myronides filum, male; nat. size.
- " 2. " binodis, male, metanotum and median segment.
- ,, 3. ,, ramulus, female; nat. size.
- ,, 4. Brachyrtacus celatus, female; nat. size.
- ,, 5. Gigantophasma pallipes, male; nat. size.
- " 6. " bicolor, female; nat. size.
  - 6a. Extremity of body, to show outline of cerci and genital operculum.

#### PLATE VIII.

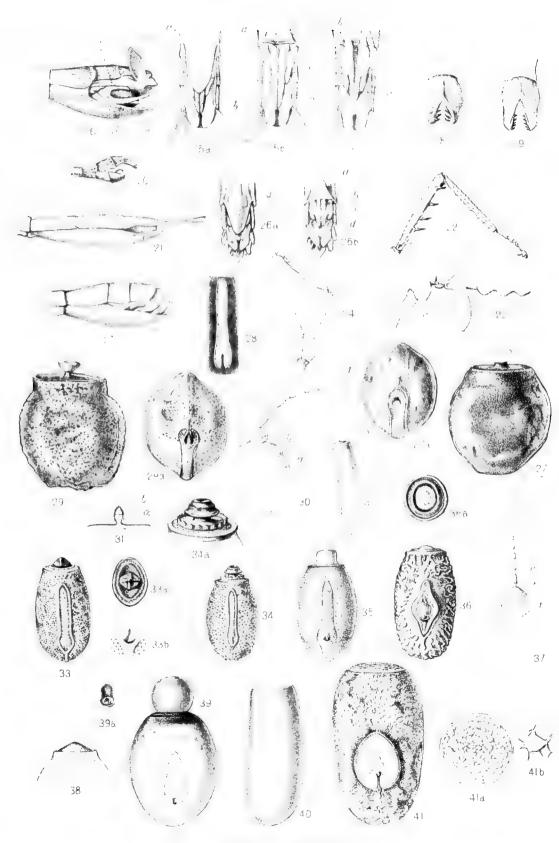
- Fig. 7. Eurycantha horrida, young (probably male).  $\times \frac{9}{8}$ .

  7a. Antenna more magnified.
  - young female.  $\times \frac{1}{1} \frac{3}{2}$ . 8a. Antenna more magnified.
- " 9. " adult male; nat. size.
- ,, 10. ,, adult male, middle of under surface of body; a, mesosternum; b, c, metasternum; d, 2nd abdominal sternite of Brunner.
- , 11. Acanthodyta spiniventris, female; nat. size.
- " 12. Cacomorpha aberrans, female; nat. size.
- ,, 13. Phyllium brachysoma, female; nat. size.
- ,, 14. Chitoniscus feejeeanus, left tegmen; nat. size.
- ,, 15. Phyllium sp. young; nat. size.

#### PLATE IX.

- Fig. 16. Anchiale stolli; extremity of body of female, with egg; a, superior (of 9th segment), b, median (of 9th segment), c, inferior (of 8th segment), processes; d, egg; e, cercus.  $\times \frac{\pi}{2}$ .
  - ,, 17. Anchiale confusa; extremity of body of female.  $\times \frac{5}{3}$ .
- " 18. Anchiale confusa; dorsal view of terminal segment of male; magnified.
- ,, 19. ,, stolli; ,, ,, ,, ,, ,,
- ., 20. Acanthodyta spiniventris; extremity of body of male.  $\times 2$ .
- ,, 21. Graeffea lifuensis; extremity of body of female. × 2.
- " 22. Gigantophasma pallipes, of hind leg; nat. size.
- ,, 23. Cacomorpha aberrans; female; side view of middle of body; a, pseudo-tracheal gill of metathorax; b, base of hind femur.  $\times 4$ .
- , 24. Phyllium brachysoma, front leg, magnified.

- Fig. 25. Anchiale stolli; female nymph, undersurface of extremity of body, to show the partially developed genital processes; 25a, the parts in their natural position; a, genital operculum formed by 8th segment; b, inferior processes (of 8th segment); c, superior processes (of 9th segment). 25b, the same with the operculum turned forwards; 25c, the same with the operculum and inferior processes turned forwards; d, median processes (of 9th segment).
  - ,, 26. Myronides sp.? female nymph, to show the partially developed genital processes; 26a, the parts in their natural position; 26b, with the operculum turned forwards; a, operculum; b, inferior processes; c, superior processes; d, median processes.
  - ,, 27. Egg of Anchiale stolli; 27a, inferior pole of same, showing hilar scar, a. × 8.
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SHARP PHASMILAR

Edwin Wilson Cambridge

# SCORPIONS, PEDIPALPI AND SPIDERS COLLECTED BY DR WILLEY IN NEW BRITAIN, THE SOLOMON ISLANDS, LOYALTY ISLANDS, ETC.

#### By R. I. POCOCK.

OF THE BRITISH MUSEUM OF NATURAL HISTORY.

#### With Plates X. and XI.

THE Arachnida forming the subject matter of the following pages are referable to 49 species. Of these a large majority (namely thirty-six) was collected in New Britain, six only being obtained in the Solomon Islands and nine in the Loyalty Archipelago and on the Isle of Pines. All the species met with in the last-mentioned localities prove referable to previously described forms; but of the six brought from the Solomon Islands two appear to be new, and of the 36 from New Britain no fewer than 14 are undescribed, so that the total number of species novae collected amounts to 16, that is to say, nearly 35 per cent. of the whole collection.

Dr Willey's researches in the Solomon Islands add three species to the list recently published by me', namely, one Scorpion (Archisometrus perfidus), one Pedipalp (Thelyphonus leucurus) and one Spider (Linus alticeps).

From the Archipelago of New Britain, including New Ireland, Duke of York Island and New Hanover, the following species had been recorded in 1881 (see Thorell, Ann. Mus. Genova, XVII., pp. 684—711):—Gasteracantha panisicca, Butl.; G. pentagona, Walck.; G. studeri, Karsch; Argiope brownii, Cambr.; Argiope picta, L. Koch; Argiope pentagona, L. Koch; Epeira trigona, L. Koch; E. gazellae, Karsch; Nephila maculata, Fab.; Heteropoda vulpina, Cambr.; Heteropoda peroniana, Walck.; Palystes ignicomus, L. Koch; P. pinnotherus, Walck. Of these 13 species, Gasteracantha panisicca, recorded by Mr O. P. Cambridge, is probably identical with the species Thorell subsequently described as G. karschii, and Heteropoda vulpina described by Mr O. P. Cambridge is, in my opinion, identical without doubt with Palystes ignicomus of L. Koch. It is further possible that the specimens referred to Argiope pentagona by Karsch are identical with those that Mr Cambridge described as A. brownii, the two species being closely related.

Keyserling subsequently recorded the following species from New Ireland:—Gaster-acantha violenta, L. Koch; G. mollusca, L. Koch; Cyclosa insulana, Costa, and Argyro-epeira grata, Guérin; and since the majority of those contained in Thorell's list also came from New Ireland or New Hanover, and the Duke of York Island, the exact locality of the specimens collected by Mr Brown being apparently doubtful, it is clear that the material brought by Dr Willey from New Britain is of considerable value from a faunistic point of view seeing that practically nothing was previously known of the Arachnid fauna of that island.

<sup>1</sup> Ann. Mag. Nat. Hist. (7), 1. pp. 457-475, 1898.

Of the 36 species obtained in the island, 14 have been described as new. With the exception of the one Attoid spider, Tarodes lineatus, which is the representative of a new genus, all the new forms belong to genera which have a wide range in the Indo and Austro-Malayan area, the only exception to the statement being furnished by the Pedipalp Abalius willeyi, from New Britain, which belongs to a genus hitherto only met with in New Guinea and Samoa. The rest of the species, too, are for the most part either widely distributed themselves over the same area or belong to widely ranging genera. In fact this collection supplies one more link in the chain of evidence which proves that so far as the Arachnida, with the exception of some of the Scorpions, are concerned there is no geographical barrier between the Oriental and Australian regions of Sclater and Wallace.

A few points of interest connected with the bionomics of some of the species remain to be mentioned. Of these perhaps the most important are Dr Willey's discovery of the cocooning habits of *Fecenia*, and of the nesting habits of *Conothele*. Attention may also be drawn to the cocoons of *Ordgarius* which, I believe, have never been hitherto described.

Lastly, there is the remarkable stridulating organ found in *Plexippus stridulator*. Stridulating organs of various structures have been found in genera of many families of Spiders, but none up to the present time in any member of the family Attidae. Moreover the organ, consisting of a series of strong ridges on the lower side of the mandible and of the serrula or finely-denticulated ridge which runs along the fore edge of the maxilla, occupies a position which is unique in the order Araneae.

List of the species obtained in New Britain:-

#### SCORPIONES.

Hormurus australasiae.

#### PEDIPALPI.

Abalius willeyi, sp. n. Sarax sarawakensis.

Encyocrypta pictipes, sp. n.

#### ARANEAE.

Conothele arboricola, sp. n.
Nephila maculata.
Argiope magnifica.
, picta.
Araneus caput-lupi.
Cyclosa insulana.
Argyroepeira grata.
, granulata.
Tetragnatha rubriventris.
Cyrtarachne tricolor.
Ordgarius bicolor, sp. n.
Gasteracantha brevispina.

Actinacantha aciculata, sp. n. Lathrodectus hasseltii. Psechrus argentatus. Fecenia angustata. Oxyopes macilentus. papuanus. Lycosa willeyi, sp. n. Ctenus rufisternus, sp. n. Heteropoda venatoria. Pandercetes plumosus, sp. n. Sparassus actaeon, sp. n. Palystes ignicomus. Thelcticopis ochracea, sp. n. Thomisus pustulosus. Diolenius lugubris. Tarodes lineatus, gen. et sp. n. Zenodorus variatus, sp. n. Bathippus proboscideus, sp. n. Plexippus stridulator, sp. n.

Gasteracantha taeniata karschii.

List of the species obtained in the Solomon Islands:-

#### SCORPIONES.

Hormurus australasiae.
" karschii.
Archisometrus perfidus.

#### PEDIPALPI.

Thelyphonus leucurus, sp. n.

# ARANEAE.

Gasteracantha signifer. Linus alticeps, sp. n.

List of the species obtained in the Loyalty Islands and the Isle of Pines:-

#### SCORPIONES.

Hormurus australasiae.

#### ARANEAE.

Nephila venosa.
" insularis.

# Argiope aetherea.

" protensa.

 $Cyrtophora\ \ cylindroides.$ 

moluccensis.

Gasteracantha westringii.

Lathrodectus hasseltii

#### ORDER. SCORPIONES.

# FAMILY. SCORPIONIDAE.

GENUS. Hormurus, Thor.

Hormurus australasiae (Fabr.).

Syst. Ent., p. 399, 1775.

Loc. New Britain; Rubiana, New Georgia in the Solomon Islands, and Maré, Lifu and Uvea in the Loyalty Islands.

Ranges from the Polynesian Islands westwards as far as Burma.

# Hormurus karschii, Keyserling.

Die Arachniden Australiens 1885, p. 31, Pl. III, Fig. 3.

Loc. Rubiana, New Georgia (Solomon Islands).

Recorded from New Guinea where the species appears to be not uncommon.

#### FAMILY. BUTHIDAE.

# GENUS. Archisometrus, Kraep.

# Archisometrus perfidus (Keyserling).

Isometrus perfidus, Keyserling, Die Arachn. Australiens 1885, p. 15, Pl. II, Fig. 2. Loc. Rubiana, New Georgia (Solomon Islands). Hitherto known only from the Fiji Islands.

#### ORDER. PEDIPALPI.

#### FAMILY. THELYPHONIDAE.

GENUS. Abalius, Kraepelin.

Abalius willeyi, sp. n.

Pl. X. Fig. 2.

Colour: a uniform deep brown above, paler below and on the extremities of the legs.

Carapace rugose throughout, also granular laterally on the thoracic portion. Tergites closely granular; sternites rugose and finely granular laterally, smooth and punctured in the middle; genital operculum punctured in the middle, granular at the sides, with a longish broad impression in the middle of its posterior half and lightly impressed on each side of the median prolongation.

Coxae of *chelae* smooth and punctured below, the process directed forwards, externally convex, internally normally shouldered: trochanters smooth below and armed with two spines, rugose and punctured above and armed with five spines, the angular the longest and the anterior longer than either of the interior spines; femur coarsely punctured below and externally, smoother above, armed with two spines, the upper very small; tibia and hand sparsely punctured, tibial process with two spinules near the apex on its posterior aspect.

Legs: tibial spur and protarsal spur on 2nd, 3rd and 4th legs; tarsus of 1st with 7th, 8th and 9th segments modified as represented in Figure 2, Pl. X.; 2nd segment not twice as long as broad, longer than 3rd, 3rd to 6th progressively decreasing in length.

Total length of carapace and abdomen not including caudal feeler 22 mm., of carapace 7.5.

Loc. New Britain.

Only two species of the genus Abalius have been hitherto described, namely, A. rohdei, Kraepelin, from Papua, and A. samoanus, Kraepelin, from Upolu. This new species is nearly allied to the latter, but certainly differs in the form of the tarsal segments of the legs of the 1st pair. In A. samoanus the 8th segment is much shorter than the 7th and much wider than long, whereas in A. willeyi the 8th is longer than the 7th and longer than its basal width, the 7th and 8th being together much longer than the 5th and 6th, and the 2nd segment only about one-third longer than the 3rd. In A. samoanus the 2nd segment is twice as long as the 3rd, and the 5th and 6th are as long as the 7th and 8th.

Keyserling's species *Thelyphonus insulanus* (Die Arachniden Austral. 1885, p. 42, Pl. IV, Fig. 2) from the Fiji Islands and New Hebrides, whence the British Museum has examples, does not belong to the genus *Abalius* as Kraepelin supposed would be likely, but to *Thelyphonus* in the strict sense of the word.

GENUS. Thelyphonus, Latr.

Thelyphonus leucurus, sp. n.

Pl. X. Fig. 1—1 a.

\$\diamsless\$. Trunk, legs and chelae a nearly uniform dark brown, with the posterior border of the tergites redder; lower side of trunk and of coxae of legs paler; tail whitish-yellow.

Carapace granular behind, roughened with wrinkles in front; the interocular area marked with four low longitudinal crests, a pair on each side of the middle line and one on each side above the ocular ridge. Upper side of abdomen granular, coarsely coriaceous between the granules, the median stria on the tergites traceable to the 8th; ventral surface coriaceous; genital plate punctured, setose, with shallow median groove and a pair of impressions.

Lower surface of coxae of chelae punctured and setose, transversely wrinkled in front towards the middle line; apex of coxal process directed forwards, the inner surface with normal and rounded shoulder; trochanter with two lower spines and six upper spines, three on the inner edge and two on the anterior edge external to the long angular spine; femur with one inferior spine and a small superior spine; upper side of trochanter and of femur coarsely punctured, wrinkled and subgranular towards the inner edge; tibia and hand smooth, coarsely but sparsely punctured; three spines on the outer edge of the tibial process, the series continued by about three more spines, inner edge of manus and of immovable digit with about nine spines.

Tarsus of 1st leg, with its 2nd segment about twice as long as wide, as long as the two succeeding segments, which like the 5th and 6th are wider than long; 8th segment enlarged, wider than long, with a longish internal distal process, 9th segment more than one-third the length of the entire tarsus, quite five times as long as wide, its basal half on the inner side widely excavated, black, the extremities of the excavation marked by a low tuberculiform elevation.

Legs externally granular; tibial and protarsal spur on the 2nd, 3rd and 4th legs. Ommatoids, small space between them equal to about four times their diameter. Tail thick.

 $\mathcal{E}$ . Differing from  $\mathfrak{P}$  in normal sexual characters; but in addition the legs are redder on their distal half, there is one moderately large bifid spine on the anterior edge of the upper surface of the trochanter, the sixth spine present in the  $\mathfrak{P}$  being absent on one side and represented on the other by a high tubercle; tibia and hand more closely punctured; chelae otherwise as in the  $\mathfrak{P}$ ; 9th tarsal segment of 1st leg scarcely as long as the sum of the 6th, 7th and 8th, the 2nd not so long as the 3rd and 4th.

Total length 27 mm., of carapace 9 mm.

Loc. Solomon Islands: Narowal (?) and Rubiana, New Georgia (?),

The genus *Thelyphonus* ranges from India and Ceylon to the Fiji Islands. This species is most nearly allied to *T. asperatus* Thorell (Ann. Mus. Genova (2), VI., p. 382, 1888) from Java and Amboina but may be at once recognised by the difference in the

structure of the tarsal segments of the legs of the 1st pair in the  $\mathfrak{P}$ , the process on the 8th segment being considerably shorter and the basal emargination of the 9th segment much longer and defined posteriorly by a distinct tuberculiform eminence (see Kraepelin, Abh. Nat. Ver. Hamburg, xv., p. 31, fig. 32 b, 1897).

#### FAMILY. TARANTULIDAE.

GENUS, Sarax, Sim.

Sarax sarawakensis (Thorell).

Charon sarawakensis, Thorell Ann. Mus. Genova (2), VI., p. 354, 1888. Sarax sarawakensis, Kraepelin, Abh. Nat. Ver. Hamburg XIII., p. 45, 1895. Loc. New Britain.

The specimens procured by Mr Willey have been compared with examples of S. brachydactylus from Luzon, kindly presented to the British Museum by Mons. Simon and with examples of the same genus collected by Mr Oates beneath stones at low water in the Andaman Islands. The specimens appear to me to be co-specific. Hence I am of opinion, with Prof. Kraepelin, that up to the present time only one species of this genus is known, namely that to which Thorell gave the name sarawakensis. This species has been hitherto recorded from the Philippine Islands, Borneo and New Guinea.

#### ORDER. ARANEAE.

#### SUBORDER. MYGALOMORPHAE.

FAMILY. BARYCHELIDAE.

Genus. Encyocrypta, Simon.

Simon, Ann. Soc. Ent. France 1888, p. 247. Pocock, Ann. Mag. Nat. Hist. (6) xvi., p. 225, 1898.

Encyocrypta pictipes, sp. n.

Pl. XI. Fig. 17.

Colour of carapace chocolate brown, sparsely covered with yellowish hairs; legs ochre brown, ringed with black, one black ring on the distal end of the femur, one on the patella, two on tibia and protarsus, one on tarsus; abdomen a dull muddy brown, indistinctly variegated with black.

Carapace about as long as patella and tibia of 4th leg and as patella, tibia and tarsus of palp; its width about as long as patella and tibia of 2nd leg, shorter than those of 1st.

Mandibles with rake consisting of shorter and longer, curved, pointed, slender spiniform teeth intermixed with the bristles; armed below on the inner side with about 12 larger and smaller teeth.

Labium without cusps, bristly; maxillae with nine or ten cusps or the anterior angle of the proximal extremity.

Sternum with marginal sigilla.

Palpi with about seven setiform spines on the inner and under side of the tibia at its distal end.

Legs: 1st and 2nd pairs without spines, with at most thickened bristles on the lower side of the distal end of the tibia; 3rd leg with one or two spines on anterior side of patella, one on anterior side of tibia and two setiform spines on lower side of tibia at its distal end; protarsus with three strong anterior spines and about three pairs of spines below, those situated along the posterior side of the lower surface setiform; 4th leg with its tibia armed below with a few setiform spines; protarsus with three strong spines in front and three below, two at the apex, as well as some spiniform setae; scopulae on palpus and on legs of 1st and 2nd pairs undivided and extending to the base of the segments; protarsus of 3rd with a few apical scopular hairs, scopula of 3rd tarsus divided; scopular hairs on 4th protarsus scarcely traceable, scopula on 4th tarsus divided by a wide band of setae; claws armed with two teeth near the middle of their length, the second posterior tooth small on the posterior legs.

Measurements in millimetres. Total length 12, length of carapace 5.5, width 4.5; length of palp 8.5, of 1st leg 12, 2nd leg 11.5, 3rd leg 11, 4th leg 15 (all measured from base of femur).

Loc. New Britain.

Judging by the colour of the legs this species most resembles *Idiommata annulipes*, Thorell (Ann. Mus. Genova XVII., p. 248, 1881), from Yule Island, New Guinea, but differs from it at least in the absence of spines from the tibia of the anterior legs.

FAMILY. CTENIZIDAE.

GENUS. Conothele, Thorell.

Ann. Mus. Genova XIII., p. 304, 1878.

Conothele arboricola, sp. n.

Pl. X. Fig. 3-3 a.

Colour of upper side a nearly uniform blackish brown; abdomen tinted with purple; lower surface paler brown.

Carapace smooth, slightly hairy laterally; with a pair of long setae on the summit, a few shorter ones between this and the ocular tubercle, two in front of the tubercle: tubercle transversely oblong; carapace about as long as wide, its length about equal to that of patella, tibia and protarsus of 1st leg, and as long as patella, tibia and half the protarsus of the 4th leg and about equal to the three distal segments of the palpus.

Mandibles with rake consisting of a single row of teeth above the socket of the fang and three or four additional teeth above the inner end of the series; armed below with ten teeth, six along the outer row, four along the inner.

Labium armed with an anterior line of six strong cusps and a pair of cusps on one side behind: maxillae armed below and on the distal angle with 35 to 40 cusps.

Palp: patella armed with two spines below, one outside, one inside: tibia and tarsus covered laterally with bands of short close-set spines.

Legs: tibiae, protarsi and tarsi of 1st and 2nd spined like the palpi, except that the apex of the tibiae on the outer side has a thick subdorsal cluster of spines continuous with those along the posterior margin; patella of 1st with two inferior external spines; patella of 3rd leg armed with 6—8 anterior spines, tibia with an anterior distal cluster of about four, and a posterior distal cluster of about the same number; protarsus with 2—2 distal spines above; and a few setiform spines below; tarsus with about five anterior distal spines and one posterior; 4th leg with a few spiniform setae on the lower side of tibia; about two slender spines on the protarsus and one or two on the distal end of the tarsus; claws of palpus with one strong basal tooth; of 1st and 2nd leg with one tooth, that on the anterior claw the larger; of 3rd with one tooth each; the anterior claw of 4th unarmed, the posterior armed with one large tooth.

Abdomen granular; from each granule arises a bristle.

Measurement in millimetres. Total length 13, length of carapace 5, of palp 9, of 1st leg 10, of 2nd leg 9, of 3rd leg 9, of 4th leg 10.8 (measured from base of femur).

Loc. New Britain.

Evidently nearly related to *C. doleschallii*, Thorell (Ann. Mus. Genova xvII., p. 237, 1881), from the Fly River, New Guinea, but differing apparently at least in the spine armature of the patellae of the 1st and 2nd legs, these segments in *C. doleschallii* being described as spined both externally and internally (in utroque margine). With *C. malayana*, Dol., from Amboina I am unable to compare it, except in so far as the little that Thorell has said concerning the latter seems to apply to this specimen from New Britain. Unfortunately neither in his description of *C. doleschallii*, nor elsewhere, so far as I can learn, does Thorell mention any characters for distinguishing that species from the previously described *C. malayana*, although a specimen of the latter was contained in his collection in 1878.

The two remaining species, namely C. birmanica, Thorell (Ann. Mus. Genova xxv., p. 19, 1887), from Burma, and C. cambridgei, Thorell (Ann. Mus. Genova xxvIII., p. 402), from Sumatra, differ from the three already discussed in having the eyes of the posterior line straight and not procurved.

A portion of the trap-door nest sent with the Spider proves that the genus Conothele, like Moggridgea, Pseudidiops and Sason, constructs its domicile upon the trunks of trees. It is a singular fact that in the Trap-door Spiders which have adopted this habit, the mandibles have quite independently acquired a subvertical position; but although this character was known to be present in Conothele, there was no direct evidence to show that it was correlated with the habit above described. Happily Mr Willey has satisfactorily settled the point. The remaining genera which constitute Simon's section Pachylomereae, namely, Pachylomerus, Cyclocosmia and Chorizops retain, so far as is known, the normal habit of digging their burrows in the ground.

#### SUBORDER. ARACHNOMORPHAE.

FAMILY. ARGIOPIDAE.

(= Epeiridae of recent authors.)

GENUS. Nephila, Leach.

Aranea maculata Fabr., Ent. Syst. II., p. 425 (1793).

Loc. New Britain.

Widely distributed throughout tropical Asia.

Mr Willey also obtained in the same island two examples of a variety of this species somewhat resembling that known as walckenaerii, and differing from the typical form in the absence of spots on the abdomen, the lower surface of which has a broad undivided yellow band extending from the vulva to the spinners and a corresponding band on the dorsal side, which, however, is divided longitudinally by darker median stripes.

Nephila venosa, L. Koch.

Verh. k.-k. zool.-bot. Ges. Wien xvii., p. 183, 1867; Die Arachn. Austral., p. 148, Pl. XII, Fig. 1 (1872).

Loc. Isle of Pines.

Previously known from Queensland, Papua, Fiji, Samoa, etc.

Nephila insularis, Keyserling.

Die Arachniden Austral. 1887, p. 215, Pl. XIX, Fig. 5.

Loc. Lifu, Loyalty Islands.

Recorded from the Loyalty Islands by Keyserling.

GENUS. Argiope, Sav. in Aud.

Argiope aetherea (Walck.).

Ins. Apt. II., p. 112, 1841.

Loc. Lifu, Loyalty Islands.

Originally recorded from New Guinea, subsequently obtained in Cape York, etc.

Argiope magnifica, L. Koch.

Die Arachniden Austral. 1871, p. 27, Pl. II, Fig. 6.

Loc. New Britain.

Dr Thorell (Ann. Mus. Genova XVII., p. 63, 1881) cites the name magnifica amongst the synonyms of A. aemula, Walck.; but examples of magnifica in the British Museum from Rockhampton and New Guinea may be recognised from examples labelled aemula by Thorell from Burma in that the yellow bands on the lower side of the abdomen meet behind and above the mamillae in a broad semicircular yellow band.

Argiope picta, L. Koch.

Die Arachniden Austral. 1871, p. 33, Pl. III, Fig. 3.

Loc. New Britain.

Recorded from Queensland, New Guinea, Aru, etc.

Argiope protensa, L. Koch.

Die Arachniden Australiens I., p. 211, Pl. XVIII, Fig. 8.

Loc. Uvea, Loyalty Islands.

Recorded by Koch from Bowen (Port Denison) in Australia.

GENUS. Araneus, Linn.

(= Epeira of recent authors.)

Araneus caput-lupi (Dol.).

Acta Soc. Sci. Indo-Neerland 1859, p. 35, Pl. VIII, Fig. 6.

Loc. New Britain.

Previously recorded from Amboina, the Moluccas, Aru, Yule Island, etc.

GENUS. Cyclosa, Menge.

Cyclosa insulana (Costa).

Cenni Zool., etc., p. 65, 1834; and of recent authors. (For synonyms, see Thorell, Ann. Mag. Nat. Hist. (6), IX., p. 232, 1892.)

Loc. New Britain.

Widely distributed in Malaysia and in the Mediterranean area of the Palæarctic Region.

GENUS. Cyrtophora, Simon.

Cyrtophora cylindroides (Walck.).

Epeira cylindroides, Walck. Ins. Apt. II., p. 136, 1837 (= viridipes, Dol., Thor. etc., nephilina, L. Koch).

Loc. Isle of Pines.

Recorded by Walckenaer from Cochin China; by Doleschall from Amboina: also known from Papua, Solomon Islands, etc.

Cyrtophora moluccensis (Dol.).

Epeira moluccensis, Doleschall, Nat. Tijdschr. Nederland-Indië XIII., p. 418, 1857; id. Acta Soc. Sci. Indo-Neerland. v., 1859, Pl. IX, Fig. 3.

Loc. Lifu, Loyalty Islands.

Ranging from India and Ceylon over the whole of Indo- and Austro-Malaysia.

GENUS. Argyroepeira, Emerton.

Argyroepeira grata (Guérin).

Epeira grata, Guérin, Voyage de la Coquille, Zool. II., 2, p. 51 (= coccinea Doleschall).

Loc. New Britain.

Previously known from Halmahera, Amboina, Ceram, Aru and New Guinea.

Argyroepeira granulata (Walck.).

Tetragnatha granulata, Walck. Ins. Apt. II., p. 222, 1841 (= Epeira orichalcea, Dol.). Loc. N. Britain,

Occurring in Celebes, Amboina, Papua, etc.

GENUS. Tetragnatha, Latr.

Tetragnatha rubriventris, Doleschall.

Tijdschr. Nederland-Indië XIII., p. 410, 1857 (see Thorell, Ann. Mus. Genova, XVII., p. 131).

Loc. New Guinea. A single specimen taken on bank of river at Igebai, Milne Bay. The species has been previously recorded from Halmahera, Amboina, Aru, Salawatty, New Guinea and Cape York.

GENUS. Cyrtarachne, Keys.

Cyrtarachne tricolor, (Dol.).

Plectana tricolor, Doleschall, Acta Soc. Sci. Indo-Neerland, p. 44, Pl. VIII, Fig. 3 (1859).

Cyrtarachne tricolor, Thorell, Ann. Mus. Genova XVII., p. 57, 1881.

Loc. New Britain. This species has been previously recorded from Celebes, Amboina, Cape York and New Guinea.

GENUS. Ordgarius, Keyserling.

Ordgarius bicolor, sp. n.

Pl. X. Figs. 4-4 a.

Colour; carapace blackish brown; abdomen deep blackish chocolate brown below, behind, at the sides, and above on the prominence, but between the prominences ornamented with a broad yellowish-brown band which behind the prominences expands to the right and left and extends over the whole of the area of upper side of the abdomen upon which there are no tubercles; legs pale yellow, annulate, there being three deep black bands on the femora and fainter ones upon the patellae, tibiae and protarsi; coxae, sternum, maxillae and labium a uniform deep blackish brown.

Carapace without spines, but strongly tuberculated, eight tubercles on the cephalic area, a pair behind, two in a line in front of the pair, the foremost on the summit of the head, and two smaller ones on each side of this lying towards the lateral ocular tubercle.

Abdomen heart-shaped, about one-third wider than long, with a pair of high, broad, rounded prominences; the prominences, the sides of the abdomen, and posterior portion of upper surface studded with rounded tubercles.

Legs unspined.

Measurements in millimetres. Total length 13, width of abdomen 12.5, length of abdomen 9.5.

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New Britain.

Allied to the Ceylonese species O. hobsoni, O. P. Cambridge (Proc. Zool. Soc. 1877, p. 562, Pl. LVI. Fig. 3), of which the British Museum has received specimens from Pundel Oya in Ceylon (E. E. Green) but differing in the smaller size and greater number of the tubercles of the abdomen, the smaller size of the median tubercle on the cephalic area of the carapace and the absence of a tubercle from the middle of the area on the upper side of the abdomen circumscribed by the four sigilla.

From the remaining three species of the genus. namely, O. sexspinosus, Thor. (Bihang Svenska Vet. Akad. Handl. xx., Pl. IV, no. 4, p. 48, 1894), from Burma, O. clypeatus, Simon (Ann. Soc. Ent. France, 1896, p. 473), from Amboina and O. monstrosus, Keyserling (Arachniden Australiens, Pt. xxxIII., p. 114, Pl. IX, Fig. 2, 1886), from Peak Downs, Queensland, O. bicolor differs in having the prominences of the carapace low and tuber-culiform, not spiniform.

The cocoon of *O. bicolor* which Mr Willey brought back, consists of a spherical case of pale yellow silk suspended at the upper end by a slender stalk of the same material and marked with irregularly arranged rows of excrescences, often of a dark brown colour, which run from the direction of the stem towards the opposite pole. Several cocoons are placed together and made to adhere one to another by threads of fine silk. Pl. X. Fig. 4 a.

GENUS. Gasteracantha, Sund.

Gasteracantha brevispina, Dol.

Tijdsche Nederland-Indië XIII., p. 423, 1857.

Loc. New Britain.

Ranging from Burma to the Fiji Islands.

Gasteracantha taeniata karschii, Thorell.

Ann. Mus. Genova (2), v. p. 230, 1887.

Loc. New Britain.

Dr Thorell based his species G. karschii upon a single example from New Britain and pointed out that it differs from the typical G. taeniata in having a single large yellow spot on each side of the ventral cone. The British Museum has an example from Mioko, off New Britain, presenting this feature; but the series of specimens obtained by Dr Willey shows that the character is inconstant. In most of the specimens, in fact there are two spots on each side of the cone as is usual in G. taeniata and its allies; but in two examples the spots are united, whereas in another they are united on one side of the cone and separated on the other. But although the character most relied upon by the describer of the species thus falls to the ground, G. karschii may, I think, be recognised as a subspecies of the Papuan taeniata by its shorter, thicker and at the same time more clavate median spines and by the anterior spines being smaller, closer to the medians and directed more forwards.

In one of the specimens the anterior black transverse band is mesially interrupted, involving only the external two sigilla, its median portion being represented

by a large black spot which involves the anterior pair of median sigilla and extends forwards to the two median sigilla of the anterior line.

Gasteracantha signifer, Pocock.

Ann. Mag. Nat. Hist. (7), I., p. 465, June, 1898.

Loc. Narowal, Solomon Islands.

Also obtained in the Solomon Archipelago by Mr C. M. Woodford and by the officers of H.M.S. Penguin.

Gasteracantha westringii, Keyserl.

Keyserling, Sitzb. Isis Dresden, 1863, p. 66. L. Koch, Die Arachniden Austral. I., p. 3, Pl. I, fig. 2, 1871.

Loc. Lifu, Loyalty Islands.

The type of this species, a dried specimen without locality, is now preserved in the British Museum. Its length as compared with its transverse width is rather less than in the examples collected by Mr Willey and the posterior spines are longer in proportion. Probably these differences are due to mode of preservation and not to natural variation.

Keyserling's collection also contained specimens of the same species, resembling those from the Loyalty Islands, from Brisbane. Curiously enough, the author did not recognise them as specifically identical with the type of his G. westringii, but identified them as G. mollusca of L. Koch. The British Museum also has dried examples labelled, though erroneously, 'Georgia.' This is perhaps a mistake for New Georgia, the name applied to one of the islands of the Solomon Archipelago, where the species very likely occurs.

GENUS. Actinacantha, Simon.

Actinacantha aciculata, sp. n.

Pl. X. Fig. 5.

Colour: carapace, mandibles, labium and maxillae black, polished, legs yellow or reddish, with brown coxae and the distal end of protarsus and tarsus black; sternum yellow with a narrow black margin; upper side of abdomen pale yellow with black sigilla, the black on the sigilla of the anterior row sometimes fused and forming a black stripe on each side, the two not uniting in the middle line, the prominences which support the spines red, spines black; the yellow of the upper surface encroaching on the lower; the lower side spotted yellow, a pair of large spots at the sides of the area between the vulva and the spinning eminence.

Abdomen pentagonal in form; the anterior spine short, directed obliquely forwards and outwards and upwards, barely half the length of the median spine, from the base of which it is separated by a space about equalling its own length; median spine longish and slender, its length about equal to the width of the head, very slender arising abruptly from the prominence that supports it and not gradually; posterior spine resembling the median but about three-fourths its length, space between the prominences of the posterior spines about equal to the length of the

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median spine and rather less than the space separating the bases of the median and posterior spine on each side. Lower side of abdomen and the prominences that bear the spines granular.

Measurements in millimetres. Total length 9, width of head 3, width of abdomen, including median spines 15, width at posterior base of anterior spines 8.5, length along the middle line of abdomen 6, length including posterior spine 8.4.

Loc. New Britain.

This species is closely allied to A. pentagona Walck. (Ins. Apt. II., p. 168; see also L. Koch, Die Arachniden p. 10, Pl. I, fig. 6) from New Ireland but has the spines considerably longer, the medians in A. pentagona, according to C. Koch's figure, being much shorter than the width of the head. The spines are also much broader at the base than in A. accidata.

Actinacantha studeri Karsch (Zeitschr. gesammt. Naturwiss. Lt., p. 799, 1878), from New Hanover is also related both to A. pentagona and A. aciculata. With A. pentagona I am unable to compare it, being acquainted with A. studeri merely from its description. It appears, however, to differ from A. aciculata in having the sternum black with a median yellow band, and the legs and palpi black with only the femora, patellae and part of the tibiae of the palpus and first two pairs of legs red.

#### FAMILY. THERIDIDAE.

GENUS. Lathrodectus, Walck.

Lathrodectus hasseltii, Thorell.

Öfv. Vet. Ahad. Forhandl. XXVII., p. 369 (1870) (= scelio, Thor.).

Loc. New Britain and the Isle of Pines.

Abundant in Australia from Cape York, southwards; also recorded from New Zealand.

#### FAMILY. PSECHRIDAE.

GENUS. Psechrus, Thor.

Ann. Mus. Genova XIII., p. 170, 1878.

Psechrus argentatus (Doleschall).

Tegenaria argentata, Doleschall, Nat. Tijdschr. Nederl. Indîë, xiii., p. 407, 1857.

Psechrus argentatus, Thorell, Ann. Mus. Genova XIII., p. 171 (1878).

Loc. New Britain.

This species has previously been recorded from Amboina, Ceram, and New Guinea (Island of Faor and the Fly River).

Allied species have been recorded from Ceylon (P. torvus, Cambr.) and Singapore (P. singaporensis, Thor.).

GENUS. Fecenia, Simon.

Bull. Soc. Ent. France, 1887, p. cxciv. (for Mezentia, Thor. preoccupied).

Fecenia angustata (Thorell).

Pl. X. Fig. 6.

Mezentia angustata, Thorell, Ann. Mus. Genova XVII., p. 204, 1881.

Loc. New Britain.

A mutilated specimen agreeing with angustata from Ternate in colour and not disagreeing with the description of it in any reliable structural features, was obtained.

Mr Willey fortunately secured this specimen when guarding its newly hatched young. The nest consists of an irregular shaped silken sac adhering tightly to the surface of a rolled leaf with one or two arched apertures (for the ingress and egress of the mother) round the margin. The edges of the leaf are held together with silk and thus form a tubular chamber for the support and protection of the nest.

This cocoon-nest is very different from the nest of *F. cylindrata* discovered by Mr Oates in Burma (see Thorell, Spiders of Burma, pp. 64—66, 1895). This nest, which according to Mr Oates is placed horizontally in the centre of the web, consists of a straight tube of silk interwoven with twigs, seeds, etc., open at its broad end but closed at the narrow opposite extremity. Since the spider found in this tube is an immature female, it is possible that the cylindrical nest is constructed for protection during the process of moulting.

Mr Willey's discovery of the cocooning habits of Fecenia are of great interest, since they fill up an important gap in our knowledge and show how the genus differs in this respect from its near ally Psechrus, which according to Mons. Simon carries the cocoon in its jaws. This difference of habit between the two is exactly paralleled by the two Heteropodine genera Sparassus and Heteropoda, the latter carrying the cocoon, the former enclosing it in a rolled leaf.

FAMILY. OXYOPIDAE.

GENUS. Oxyopes, Latr.

Oxyopes macilentus, L. Koch.

L. Koch, Die Arachniden Austral. II., p. 1000, Pl. LXXXVII, Figs. 4-5.

Thorell, Ann. Mus. Genova XVII., pp. 393-395, 1881.

Loc. New Britain.

This species has been recorded by Koch from Cape York, Gayndah, Bowen, Port Mackay and Rockhampton in Australia and by Thorell from Arfak and Ramoi in New Guinea.

The specimens (3, 2) collected by Mr Willey have been compared with authentically-named examples from Rockhampton contained in the Keyserling collection. They appear to me to be specifically identical, and since the occurrence of this species in New Britain is thus substantiated, there can be no reason for doubting the accuracy of Thorell's determination of the Papuan form as macilentus.

Oxyopes papuanus, Thorell.

Pl. X. Fig. 7.

Ann. Mus. Genova, XVII., pp. 395-399, 1881.

Loc. New Britain.

A single female example referred to O. papuanus agrees with the description of the latter sufficiently closely to make the identification probably correct. Thorell has recorded papuanus from Andai, Ramoi, and Dorei Hum in Papua, from Wokan in the Aru Islands and from Cape York in Australia.

The cocoon of this species consists of a subspherical silken sac attached to the tip of the folded termination of a branch of the inflorescence of a mallow-like plant probably referable to *Triumfetta*.

FAMILY. LYCOSIDAE.

GENUS. Lycosa, Latr.

Lycosa willeyi, sp. n.

Pl. X. Fig. 8.

Colour: carapace piceous or deep castaneous with a pale median dorsal band and a lateral band of about the same width, the dark intervening area crossed by narrow radiating flavous stripes; maxillae, labium and mandibles black, the latter clothed with flavous hairs; sternum and coxae ochraceous; legs and palpi ochraceous, covered with flavous hairs; the scopulae fuscous and the spines black; abdomen uniformly dirty yellow below; a deeper ochre yellow finely speckled with black above, with indistinct traces of a short anterior median darker stripe.

Carapace a little longer than patella and tibia of 4th leg, slightly excelling tibia and protarsus of 1st leg, and a little less than protarsus and half the tarsus of the 4th leg; eyes of anterior line a little narrower than those of the median, a little procurved, the medians larger than the laterals and separated from the edge of the clypeus by a space which slightly exceeds their diameter, the distance between the medians less than their diameter; distance between eyes of 2nd line a little less than their diameter.

Palpi: femur with 1, 1, 4 spines above; patella with 1 internal setiform spine; tibia with 3 and tarsus with 4 setiform spines.

Legs: 1, 2, 3, 4 in length, 2nd and 3rd nearly equal; femur of 1st armed above with 7 spines, 2 of them being internal and apical; patella unarmed; tibia with 2, 2, 2 weak spines below, protarsus armed below with 2, 2, 1 spines amongst the scopular hairs and 1, 1 at the apex above the scopula; 2nd leg armed like the 1st except that the 2 spines on the anterior side of the upper surface of the femur are separated, not close together; 3rd and 4th legs with patella armed with 1, 1 spine, tibia armed with 2, 2, 2 spines below, 2 in front, 2 above, and 2 behind, the protarsi armed with about 12 spines arranged in 4 rows of 3 each, those on the lower side of the 4th protarsus not so noticeably arranged in series.

Vulva (as in figure).

Measurements in millimetres. Total length 19, length of carapace 10, of 1st leg 22, 2nd leg 21, 3rd leg 28, 4th leg 28.

Loc. New Britain.

With the eyes of the anterior row a little narrower than those of the median, the abdomen uniformly yellow below, two spines on the upper side of the tibia of the 3rd and 4th legs, the patellae of the 1st and 2nd pairs without spines, the anterior median eyes larger than the anterior lateral, the protarsus of the 4th leg shorter than the patella and tibia of this limb and the carapace ornamented with median and lateral bands, Lycosa willeyi falls alongside of L. pulvere-sparsa of L. Koch (Die Arachniden Austral. II., pp. 895 and 941, Pl. LXXXI., Fig. 6, 1877 and 1878) from Rockhampton, but certainly differs from it, at least in the form of the vulva, the excavation of the epigynal plate being much broader, the cross-bar of the median piece much longer, etc.

FAMILY, CTENIDAE.

GENUS. Ctenus, Walck.

Ctenus rufisternus, sp. n.

Pl. X. Fig. 9-9 a.

Colour: (dry) carapace clothed laterally with dark yellowish hairs, naked above but showing traces here and there and just behind the eyes of having been covered with silvery white hairs; mandibles, palpi and limbs clothed with dirty yellowish hairs, those on the tibia of the 1st and 2nd legs silver white, and those on the tibiae and protarsi of 3rd and 4th yellowish white; hairs of abdomen greyish black, with a broad pale band in the dorsal middle line and spots of silvery hairs below; integument of cephalothorax and legs (in alcohol) blackish, with a broad reddish line in the dorsal middle line; sternum and coxae bright yellowish red.

Carapace higher behind than in front, a nearly even slope from the posterior to the anterior edge of the upper surface; a little shorter than patella and tibia of 1st leg and a little longer than those of 2nd, a little longer than 4th protarsus. Eyes: ocular quadrangle wider than long, narrower in front than behind; anterior median eyes smaller than posterior median and closer together, space between them about equal to their radius; eyes of second row a little procurved, the lower edge of the laterals slightly below the level of the lower margin of the medians; the anterior laterals oval, separated from posterior medians by a space about equalling their long diameter; clypeus short, less than radius of anterior centrals.

Legs: femur of 1st armed with 11 spines, arranged in rows approximately 4, 3, 4; patella, spines 1, 1; tibia armed with 5 pairs below, 2 in front, 3 above, and 2 behind; protarsus armed with 12 spines 3, 3, 3, 3; with or without an additional median spine above; 2nd leg armed apparently as the 1st; 3rd leg, femur with about 11 spines; tibia with 3 pairs below, 2 spines in front, 3 above, and 2 behind; protarsus with 3 pairs below, 3 spines in front, 3 behind, with 1 extra above and 1 at the apex; 4th leg armed like the 3rd, with about 15 spines more irregularly arranged than on the other legs.

Palp with tibia about as long as patella and armed externally with a quadrate process, the upper edge of which is convex, the lower straight; a spiniform process on its distal margin; palpal organ as in figure.

Measurements in millimetres. Total length 12, length of carapace 7.2, width 5, length of 1st leg 18, of 2nd 15, of 3rd 13.5, of 4th 19.2.

Loc. New Britain.

Easily distinguishable from *C. agalenoides*, L. Koch, from Gayndah, and *C. agrœcoides*, Thorell, from Cape York, by its red coxae and sternum, absence of distinct rings on the legs, and also from the former in the form of the palpal organ, etc.

FAMILY. HETEROPODIDAE.

GENUS. Heteropoda, Latr.

Heteropoda venatoria (Linn.).

A single specimen of this, the common large house-spider of the tropics, was collected in New Britain.

GENUS. Pandercetes, L. Koch.

Pandercetes plumosus, sp. n.

Pl. X. Fig. 10.

Colour: (dry) carapace and abdomen covered above with whitish hairs intermixed with yellow, the hairs around the eyes tinted with brown and those on the carapace behind the head with pale green; hairs on upper side of abdomen rubbed away; hairs on legs yellowish white, developed into long fringes, especially on the femora, as in P. plumipes; (in alcohol), the carapace, legs and abdomen are testaceous, mottled with black, the legs being very noticeably spotted with blackish grey, the blackish spines showing up strongly; labium and maxillae and tip of mandibles ferruginous; sternum coxae and under side of legs entirely testaceous yellow; 3rd leg with an elongate black spot at base of femur and a long black line traversing the whole of the lower side of the tibia and protarsus.

Carapace about as wide as long, about as long as protarsus of 3rd leg.

Palpi: femur armed with 4 spines; patella with 1, 1; tibia with 3 inner, 1 upper, 2 outer; tarsus with 3 inner and 3 outer. Legs: femur of 1st leg with 3, 3, 3 spines, patella with 1 posterior spine; tibia with 4 pairs of long spines beneath; protarsus with 3 pairs of spines, one pair being situated above close to base; 2nd leg armed like 1st; 3rd leg femur with 3, 3, 2 spines, tibia with 2, 2 spines beneath and 1 anterior and 1 or 2 posterior spines, protarsus with 2, 2 inferior spines and 1 anterior basal spine; 4th leg spined much as the 2nd but less regularly, femur with only 1 posterior spine; tibia and protarsus with 5 spines.

Vulva consisting of a sub-oblong plate, hairy at the sides and marked mesially with a longitudinal groove which anteriorly expands into a longitudinally oval depression.

Measurements in millimetres. Total length 14, length of carapace 6, of 1st leg 29, of 2nd 29, of 3rd 22, of 4th 26; length of femur of 2nd 8.6.

Loc. New Britain.

This species certainly differs from Pandercetes plumipes of Doleschall from Amboina (Acta Soc. Sci. Indo. Neerland, 1859, p. 53, pl. III., fig. 9), which it resembles in plumosity, at least in having much shorter legs; for example, judging by Doleschall's figure, the femur of the 2nd leg in plumipes is about twice as long as the carapace (7:14), whereas in P. plumosus the femur is only once and a half times the length (6:8.6). From P. isopus, Thorell, from Fly River, New Guinea (Ann. Mus. Genova. xvII., pp. 308, etc.), it differs in having the legs much longer as compared to the carapace, the proportion between the 1st leg and the carapace being 29:6, whereas in isopus the proportion is  $24\frac{3}{4}$ :6. Moreover the leg measurements given by Thorell probably include the trochanter and part of the coxae, so that the difference is no doubt even greater than appears at first sight.

GENUS. Sparassus, Latr.

Sparassus actaeon, sp. n.

Pl. X. Fig. 12.

Q Colour: hairy clothing of limbs and carapace a rich ochre or golden yellow; upper side of head and anterior surface of mandibles rubbed smooth; sternum very scantily clothed, upper side of abdomen much the same colour but rather darker; lower side darkish brown with four faint pale stripes passing from the epigastric fold to the spinners: integument of carapace and limbs a deep chestnut brown, mandibles, maxillae, labium and sternum black.

Carapace longer than broad, moderately high, its length equal to that of tibia of the 1st leg and a little less than its protarsus; less than tibia of 2nd, less than patella and tibia of 3rd, about equal to tarsus and protarsus of 3rd; its width just equal to protarsus of 4th. Eyes of posterior line straight, the medians smaller than the laterals and a little nearer to each other than either is to the corresponding lateral; ocular quadrangle a little wider behind than in front; anterior median eyes separated by a space, which is less than their diameter and nearer to each other than either is to the lateral; clypeus a little less than the diameter of anterior median eye.

Mandibles moderately strongly geniculate at the base.

Legs: long; 2, 1, 4, 3; the 2nd from the base of the femur more than four times as long as the carapace; 2nd exceeding the 1st by the length of the tarsus and the 3rd by the length of the tarsus and  $\frac{4}{5}$  of the protarsus: 1st leg, femur with 9 or 10 spines above, patella with spines 1, 1, tibia with 2, 2, 2 below, 2 in front and 2 behind; protarsus with 2, 2 below, 2 in front, and 2 behind; 2nd leg spined like the 1st, the femur irregularly; 3rd leg like the 2nd, 4th leg with only an anterior patellar spine.

Vulva consisting of a chitinous plate marked with two arched grooves running longitudinally, approaching each other but not meeting in the middle line in front and circumscribing a heart-shaped area which shows a median depression.

Measurements in millimetres. Total length 34, length of carapace 17, width 15, length of 1st leg 67, of 2nd 72, of 3rd 51, of 4th 55.

Loc. New Britain.

According to L. Koch's tables of Australian species of *Sparassus* this new form falls under the heading and alongside of *S. nitelinus* from Peak Downs, a species which it also somewhat resembles in the form of the vulva. *S. actaeon* certainly differs, however, in being much larger, differently coloured and in possessing much longer legs.

Genus. Palystes, L. Koch.

Palystes ignicomus, L. Koch.

Palystes ignicomus, L. Koch, Die Arachniden II., p. 701, pl. Lx., figs. 2—20, 1875. Sarotes vulpinus, O. P. Cambridge, Proc. Zool. Soc. 1877, p. 286.

Loc. New Britain.

The specimen of the species described by Dr Koch was collected in New Ireland. The type of vulpinus, which Mr Cambridge has kindly sent to me for examination, was obtained by the Rev. George Brown either in the Duke of York Island or on the adjacent coasts of New Ireland or New Britain. Although this specimen is a not quite adult female, I have no hesitation in regarding it as specifically identical with P. ignicomus, of which Mr Willey obtained some beautifully coloured examples (A, P).

GENUS. Thelcticopis, Karsch.

Thelcticopis ochracea, sp. n.

Pl. X. Fig. 11.

Colour: carapace, sternum, and legs a nearly uniform pale castaneous tint, legs paler than carapace, both scantily clothed with greyish white hairs; abdomen a pale mouse grey with a series of indistinct median spots above and short oblique stripes of the same tint on each side; mandibles deep brown.

Carapace about as long as patella and tibia of 4th leg, a little shorter than those of 2nd leg. Mandibles moderately strongly geniculate. Palpi with tarsus apically scopulate, its femur armed apically with 5 spines, patella with 1 anterior and 1 posterior spine, tibia with 3 anterior, 1 superior and 2 posterior spines, tarsus with 3 anterior (inner) and 3 posterior (outer).

Legs: 1st, 2nd and 4th nearly equal; femur of 1st armed with 1 or 2 anterior, 1 superior and 3 posterior spines, patella unarmed, tibia with 6 pairs of inferior spines, protarsus with 1 pair of inferior spines; 2nd leg, femur with 3, 2, 3 spines, tibia with 5 pairs of inferior spines; 3rd leg, femur with 3, 2, 1 superior spines; tibia, 3 pairs of inferior spines, and 1 anterior spine; 4th leg as in 3rd, but the tibia armed in addition with 2 interior and 2 posterior spines, and the protarsus with 2 pairs of inferior spines, 3 anterior and 3 posterior; tibiae of 1st and 2nd leg very slightly scopulate anteriorly.

Vulva consisting of a large plate deeply hollowed out, the margin of the excavation semicircularly concave in front, produced posteriorly and laterally into a rounded prominence on each side, and ending behind in a pair of narrowed apically rounded processes projecting beyond the hinder border of the median sclerite, which consists of a pair of smooth shining bosses united posteriorly and ending in a small subquadrate prominence.

Measurements in millimetres. Total length 15.5, carapace 6.8, length of 1st leg 20, of 2nd 19.5, of 3rd 15.5, of 4th 19.5.

Loc. New Britain. A single ? example was obtained.

In its small size this species approaches *T. birmanica*, Thorell, from Burma, and *T. flavipes*, Pocock, from Batjan, but certainly differs from both in the form of the vulva. In *T. birmanica* the lateral portions of this organ end posteriorly in a pair of relatively widely rounded skeletal pieces and are not narrowed and produced as in the other two. Again in *T. flavipes* the median sclerite consists of two elongate ridges, ending behind in a narrow process which projects beyond the apices of the lateral pieces.

#### FAMILY. THOMISIDAE.

GENUS. Thomisus.

Thomisus pustulosus (L. Koch).

Xysticus (Musumena) pustulosus, L. Koch, Verh. zool.-bot. Ges. Wien, xvII., p. 220, 1867; id. Die Arachniden Austral. I., p. 531, pl. 40, fig. 6, 1874.

Pistius pustulosus, Thorell, Ann. Mus. Genova, XVII., p. 331, 1881.

Loc. New Britain.

This flower-frequenting species is evidently not uncommon in parts of Queensland, the British Museum possessing specimens from Rockhampton, Herbert River, etc. L. Koch has recorded it from Cape York, Bowen, Brisbane, etc., and Thorell from the Kei and Aru Islands and from Papua.

#### FAMILY. ATTIDAE.

GENUS. Diolenius, Thor.

Diolenius lugubris, Thorell.

Ann. Mus. Genova, XVII., p. 414, 1881.

A single female of this or of a closely allied species was collected. The type of D. lugubris, a male, was obtained at Ramoi, in New Guinea.

#### Tarodes, gen. nov.

Carapace low, longer than wide, flat above, the cephalic region not or scarcely higher than the thoracic, the posterior fifth abruptly sloped downwards close up to the fore-part of the abdomen which is in contact with it or abuts against it; cephalic portion a little shorter than thoracic. Ocular area perhaps a little wider than long, parallel sided, eyes of the 2nd row equidistant from those of the 3rd and 1st, and in the same line with them; clypeus linear; the anterior eyes nearly in contact, the upper edge of the laterals on a level with the upper edge of the medians.

Mandibles small and vertical; labium much longer than wide; maxillae of medium

length, distally expanded.

Sternum convex, oval but narrowed behind, with its margin strongly excavated,

ending posteriorly in a blunt extremity, and not passing between the 4th coxae.

Legs: 1st pair large, with coxae and trochanter long, the coxae much longer and stouter than those of the rest of the legs; trochanter slender, cylindrical, but distinctly though not much longer than the coxae; femora much longer than trochanter, thick and curved; patellae shorter than femora and about half the length of the tibiae, which

are much thickened and hairy and spiny below; protarsus slender, not half as long as the tibia and spiny below. The remaining legs short, the 4th longer than the 3rd, and the 3rd than the 2nd.

Abdomen narrow and elongate.

This genus seems to stand near  $Tara^1$  of Peckham (= Atrytone, Keyserling<sup>2</sup>); but is certainly different in having the tibia of the 1st leg inflated.

Tarodes lineatus, sp. n.

Pl. XI. Fig. 13.

Colour: carapace mahogany brown with black pigment around the eyes; scantily clothed above with yellowish white hairs which form a thicker whitish stripe in the middle line, a broad yellowish white band passing along the side below the eyes and a white marginal band; hair in neighbourhood of eyes with a distinct reddish tinge; abdomen covered above with yellowish white hairs; its integument yellow with four longitudinal black bands running from the fore-part past the middle, and posteriorly breaking up into or giving place to short obliquely transverse black stripes. The two black bands on each side united in front and closer together than are the two admedian bands; between the posterior extremities of the latter there is a median black stripe; lower side of abdomen not clothed with white hairs, blackish; 2nd, 3rd and 4th legs yellow, the 3rd and 4th distally faintly banded with black; sternum, labium, mandibles, maxillae, palpi and greater part of 1st legs piceous or mahogany; the protarsi and tarsi of 1st legs flavous; the upper side of the femora and patellae paler than the inner and lower, and clothed with yellow hairs.

Carapace longer than patella and tibia of 4th, shorter than those of 1st.

Mandibles short, a little longer than the front of the carapace, geniculate at the base, flat in front and rugose; fang groove armed with 2+2 teeth, fang short. Palpi shorter than carapace; the femur armed with 1 upper apical spine; patella a little longer than tibia; tibia not twice as long as broad, armed externally with a broad bifid spur; tarsus nearly as long as patella and tibia, piriform, apex truncate but thickly hairy; palpal organ consisting of a somewhat oval horny coriaceous disk ending distally in a small hooked process lying transversely, the apex of the hook directed internally.

Legs of 1st pair rugose, coxae about twice as long as broad; trochanter four or perhaps five times as long as broad; femur with upper edge strongly convex; tibia armed below with 7 internal and 5 or 6 external spines, all strong and of medium length; protarsus armed with 2 internal and 3 external spines. Femora of legs 2-4 armed apically with about three spines, femur of 2nd thickened, tibia of 2nd with 3 inferior spines, its protarsus with 2 apical and 1 further behind; tibia of 3rd with 1 apical, of 4th with 2 apical; protarsus of 4th with an apical cluster of spinuliform setae.

Abdomen more than twice as long as broad, with a thickish tuft of upright hairs on its anterior extremity.

Measurements in millimetres. Total length 5.8; length of carapace 2.5, width 1.8; patella and tibia of 1st leg 3, of 4th 1.5.

Loc. New Britain. A single male example.

<sup>1</sup> Tr. Wisconsin Acad. Sci. vi. (1886), p. 272.

<sup>&</sup>lt;sup>2</sup> Keyserling, in L. Koch's Die Arachniden Australien, 11. p. 1378, pl. cxvi. p. 6.

GENUS. Linus, Peckham.

Sinis, Thorell, Ann. Mus. Genova, XIII. p. 269, 1878 (preoccupied). Linus, Peckham, Trans. Wisconsin Acad. 1885, p. 264.

Linus alticeps, sp. n. Pl. XI. Fig. 14.

A detailed description of the new species is unnecessary since the differences that obtain between it and L. fimbriatus (Dol.) may be briefly expressed in tabular form as follows.

- b. Carapace with posterior cephalic angle nearly square, only a little obtuse, the upper surface of the cephalic portion being much more strongly raised behind; the whole carapace shorter as compared with its height; the height along a line taken through posterior eye to a point between the 2nd and 3rd coxae exceeding the length of the tibia of 1st leg and about equal to that of tibia of 4th leg. ......alticeps, sp. n.

Measurements in millimetres of L. alticeps. Total length 7.5; length of carapace from posterior border to anterior eye 3.8; height from posterior border to summit of head 3.3; vertical height from posterior eye 2.8; length of legs (from base of femur), 1st 11, 2nd 10, 3rd 9, 4th 13.5 (patella and tibia of 4th 4.5; tarsus and protarsus 5.5; patella and tibia of 1st 4).

Loc. Rubiana, New Georgia (Solomon Islands).

For comparison with the single adult female of *L. alticeps* obtained by Mr Willey, I have in my hands a single adult female identified by Dr Thorell as *L. fimbriatus*, Dol., which was collected by Sig. Beccari in Sumatra. According to Thorell *L. fimbriatus* ranges from Sumatra through Amboina and Papua to Cape York. For descriptions of the species reference may be made to: Doleschall, Nat. Soc. Sci. Indo-Neerland, 1859, p. 22, pl. v. fig. 8; Thorell, Ann. Mus. Genova, XIII. p. 269, etc., 1878, and *id. op. cit.* XXXI. p. 352, 1892.

L. labiatus, Thorell, from Burma and Java, has apparently the same form of carapace in the female as L. fimbriatus.

GENUS. Zenodorus, Peckham.

Ephippus, Thorell, Ann. Mus. Genova, XVII. p. 643, 1881 (preoccupied). Zenodorus, Peckham, Tr. Wisconsin Acad. VI. p. 297, 1885.

Zenodorus variatus, sp. n.

Carapace black, with a paler transversely arched area behind the posterior eyes; a patch of golden metallic hairs behind these eyes and more of the same colour on the areas between the eyes; a conspicuous marginal band of white hairs on the posterior half of the sides of the carapace; mandibles, maxillae and labium black, palpi yellow with tarsus blackish; legs of 1st and 2nd pairs reddish brown, with

tarsus and basal half of patella clear yellow and distal two-thirds of protarsus black; 3rd leg with coxa and trochanter yellow, femur reddish brown, paler distally, the rest of the segments yellowish with darker apices; 4th leg coloured like the 3rd but with basal half of femur and patella paler, protarsus annulate; abdomen blackish, with a pair of large spots formed of metallic golden scales on the fore part and two narrower transverse bands of the same tint behind, one in the middle the other at the posterior end.

In its structural characters this species stands near Z. juliae, Thorell; but differs in having the clypeus, that is to say, the area between the anterior eyes and the thickened marginal rim, less than half the diameter of the median eyes, only 3 long spines, instead of 6 shorter ones, upon the distal inferior apex of the tibia of the 1st leg, and no spines on the patellae of the 1st and 2nd.

Measurements in millimetres. Total length 7.5; length of carapace 4, width 3.2; length of 1st leg 9, of 2nd 7, of 3rd 11, of 4th 8, patella and tibia of 3rd 3.6, of 1st 4.

Loc. New Britain. A single adult male.

Differs from both Z. juliae and Z. d'urvillei in having the legs much more distinctly variegated, the clypeus lower and the presence of only 3 spines on the lower side of the distal end of the 1st tibia.

Genus. Bathippus, Thor.

Bathippus proboscideus, sp. n.

Pl. XI. Fig. 15.

Colour: carapace pale castaneous, black close to eyes, with white hairs and a few red ones below the eyes and on each side of the anterior eyes, the rest naked; mandibles yellowish brown with steel blue polish internally; palpi uniformly yellow; legs yellowish, femora brown, with metallic polish outside and inside; coxae of 1st and 2nd black in front; tibia and protarsus of 1st also sometimes blackish; maxillae and labium blackish, sternum pale; abdomen pale at the sides, with a broad black band above and below.

Carapace about as long as tibia of 1st leg, scarcely two-thirds the length of the basal segment of the mandible. Basal segment of mandible about five times as long as thick, armed with two spiniform teeth near the base and four teeth nearer the extremity, two of these are quite at the end, one on each side of the base of the fang, the inner one smaller and tubercular, the outer one much larger and bearing an external nodule; of the remaining teeth one, the external, is of moderate size and spiniform and stands about one-third of the distance from the end, while the other, farther forwards and on the inner side, is long, strong and slightly arched; the fang, which extends back as far as the spiniform teeth of the basal segment, is bent at an acute angle close to its base and armed internally on the distal side of the angle with a longish spiniform tooth. Distal external angle of maxillae rounded.

Palpi long and slender, the tibia at least one-third longer than either tarsus or patella.

Legs armed with long spines; patellae with an anterior and a posterior spine.

Measurements in millimetres. Total length of body 10.5; length of carapace (not including eyes) 4, width 3.3; length of basal segment of mandible 7.2, of fang from its basal angle 7.8, of palp 5.8, of 1st leg 16.5, of 2nd 12.8, of 3rd 14.8, of 4th 13.8.

Loc. New Britain. Several male examples.

In the shape and great length of its mandibles, of which the basal segment is considerably longer than the carapace, this species resembles B. montrouzieri, Lucas from New Caledonia (Rev. Mag. Zool., 1869, p. 208, pl. II. figs. 8—12) and B. montrouzieri papuanus, Thorell (Ann. Mus. Genova, XVII. p. 526), of which the British Museum possesses specimens from Aru Island and the Fly River, Papua. B. proboscideus, however, may be at once recognised by the presence of a longish tooth at the base of the fang, which is strongly angled; by the small size of the apical tooth on the inner side of the basal segment, and by the concavity of the upper and convexity of the lower side of the segment.

GENUS. Plexippus (C. Koch), Thorell.

Plexippus stridulator, sp. n.

Pl. XI. Figs. 16—16 c.

¿. Colour: carapace yellowish brown, the head region darker, redder, sometimes a paler median band on the thoracic portion; the region of the eyes clothed with hairs of a rusty red, traces of hairs of the same colour visible here and there on the thoracic portion, which like the area below the eyes is clothed with white hairs; mandibles dark, metallic, with a clothing of long white hairs; palpi and legs reddish brown, the anterior two pairs with bluish metallic lustre, tarsus and distal half of protarsus pale yellow; maxillae and labium deep brown, sternum and coxae flavous; abdomen with a pale median dorsal band with border sinuous and set off with black spots; sides of abdomen fuscous above, pale below, with a dark median ventral stripe; sides of abdomen clothed with snow-white hairs, intermixed with those of a bronzy hue above.

Carapace equal to length of patella and tibia of 2nd leg. Mandibles vertical, shorter than carapace, diverging from the base, the inner distal angle at the base of the fang produced into an elongate conical tooth; the fang-groove armed in front near the base with two spiniform teeth and behind with one long sharp spike and, at the base of the fang, a small conical tooth; on the posterior surface of the mandible there is a submedian vertical series of about 12 short strong ridges; fang moderately long, sinuous. Maxillae about twice as long as the labium, their distal portion produced externally into a strong acute angle of about 70 degrees, the margin between the angle and the scopulate oral margin straight; on the upper surface of the maxillae the serrula extends along the border to the external angle; patella and tarsus of palp subequal in length, tibia longer than either and armed externally and distally with a long straight spine.

Legs: tibia of 1st thickly hairy below and armed with 2, 2, 2 long spines and 1 anterior distal spine; protarsus of 1st and 2nd with 2, 2 spines; tibia of 2nd with 1 (posterior), 2, 2 spines below and 3 spines in front: patella of 1st without spines, of 2nd with 1 anterior spine, of 3rd and 4th with 1, 1 spines; femora with 5—7 spines above; tibia and protarsus of 3rd and 4th with many spines.

Measurements in millimetres. Total length 11.5; length of carapace 5, width 4; length of basal segment of mandible 2, of palp 5, of 1st leg 14, 2nd leg 11, 3rd leg 12, 4th leg 11.5.

Loc. New Britain.

This interesting new species of which unfortunately the male only is known is sufficiently characterised by the possession of the stridulating organ, consisting of a series of ridges on the lower side of the mandible which are scraped against the 'serrula' on the edge of the maxilla.

#### EXPLANATION OF PLATES X. AND XI.

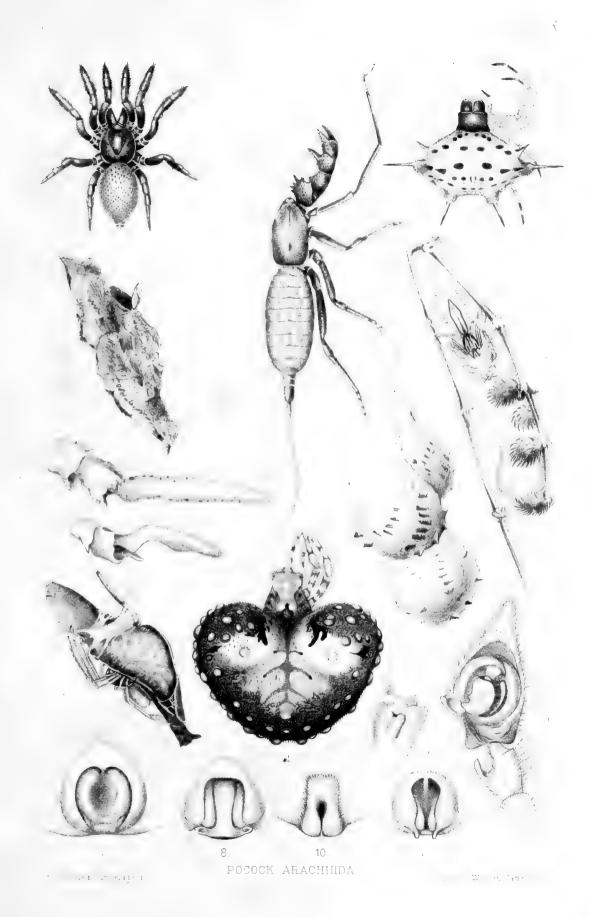
- Fig. 1. Thelyphonus lencurus, sp. n. Q. Dorsal view.
  - 1 a. , Under side of distal segments of tarsus of 1st leg of the right side.
  - 2. Abolius willeyi, sp. n. Dorsal view of distal segments of tarsus of 1st leg of the right side.
  - 3. Conothele arboricola, sp. n. Q. Nat. size.
  - 3 a. , , Trap-door nest on bark of tree. Nat. size.

(The specimen from which the figure is drawn has no lid covering the aperture of the nest. On the assumption, however, that the lid was accidentally broken away or that the nest was incomplete at the time of discovery, I have ventured to have the structure represented as in fig. 3 a. Nevertheless the possibility that Conothele habitually leaves the orifice of her nest exposed must be borne in mind. R. I. P.).

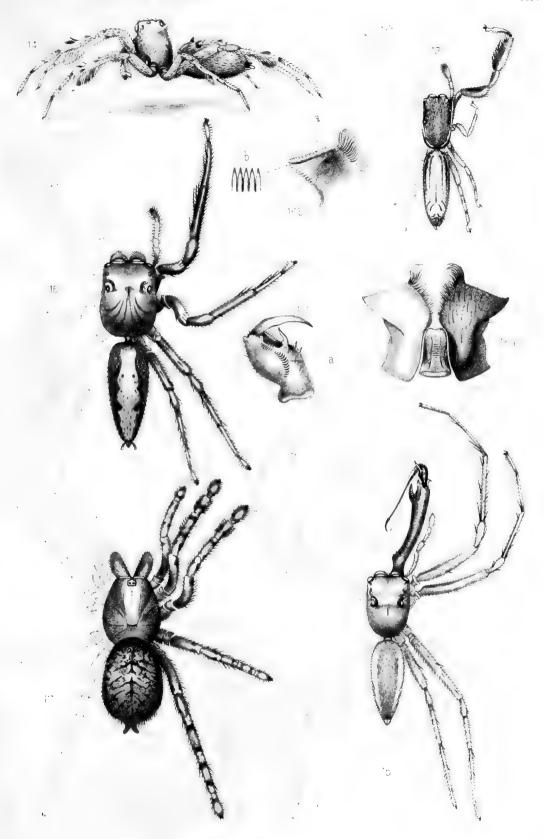
- 4. Ordgarius bicolor, sp. n. Q. × almost 4 times.
- 4 a. ,, Cluster of cocoons.
- 5. Actinacantha aciculata, sp. n.  $\mathfrak{P}$ .  $\times 2$ .
- 6. Feenia augustata, Thor. Spider on lower side of rolled leaf cut away to show the enclosed cocoon: natural size.
- 7. Oxyopes papuanus, with its cocoon in the bent stem of a mallow-like plant (? Trium-fetta).
- 8. Lycosa willeyi, sp. n. Vulva.
- 9. Ctenus rufisternus, sp. n. Palpus of & from below.
- 9 a. " Tibia and base of tarsus of palp to show tibial spur.
- 10. Pandercetes plumosus, sp. n. Vulva.
- 11. Thelcticopis ochracea, sp. n. Vulva.
- 12. Sparassus actason, sp. n. Vulva.
- 13. Tarodes lineatus, gen. et sp. n. ♀.
- 14. Linus alticeps, sp. n. Q. Lateral view.
- 15. Bathippus proboscideus, sp. n. J. Dorsal view.
- 16. Plexippus stridulator, sp. n. J. Dorsal view.
- 16 a. , , Maxillae and labium from below.
- 16 b. .. .. .. Inner surface of left maxilla showing the serrula

  (a) extending along its distal margin and an enlargement of the teeth of the serrula (b).
- 16 c. "

  Lower side of right mandible showing the series of stridulatory ridges (a).
- 17. Lecyocrapta pictipes, sp. n. 9. × 3.







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BASED ON MATERIAL COLLECTED IN

# NEW BRITAIN, NEW GUINEA, LOYALTY ISLANDS AND ELSEWHERE.

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## ZOOLOGICAL RESULTS

#### BASED ON MATERIAL FROM

# NEW BRITAIN, NEW GUINEA, LOYALTY ISLANDS AND ELSEWHERE,

COLLECTED

DURING THE YEARS 1895, 1896 AND 1897,

BY

ARTHUR WILLEY, D.Sc. Lond., Hon. M.A. CANTAB.

BALFOUR STUDENT OF THE UNIVERSITY OF CAMBRIDGE.

PART II.

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## REPORT ON THE SPECIMENS OF THE GENUS MILLEPORA COLLECTED BY DR WILLEY.

#### BY SYDNEY J. HICKSON, M.A., D.Sc., F.R.S.

Beyer Professor of Zoology in the Owens College, Manchester.

#### With Plates XII—XVI.

THE collection of specimens of Millepora brought home by Dr Willey consisted of a few very fine dried specimens, numerous fragments and a number of pieces preserved in spirit. It is of interest as exhibiting another example of the great variation in the form of growth which is a characteristic feature of the genus.

A careful examination of all the dried specimens failed to disclose any ampullae, and in none of the samples of the preserved specimens which I have examined can any trace be found of sexual organs. Many of the specimens are very considerably affected by parasites of various kinds, the details of which are given below.

Some of the specimens are modified in form by being simply thin encrusting plates which have grown over dead corals. In a recently published paper (1898) I have pointed out the evidence that there is for believing that at present only one species of the genus Millepora is known. The evidence was obtained from the study of Millepores brought from many different reefs in widely separated parts of the world, and, as Dr Willey's collection assisted me materially in the investigation which led to the publication of that paper, it is hardly necessary to repeat that in my opinion all the specimens in his collection belong to the one species *M. alcicornis* Linn.

Some of the specimens however require special description, and the question arises in what manner such specimens can be named without breaking up the genus into artificial groups and calling such groups "species," a plan which in my opinion is misleading, or on the other hand calling the old species "varieties" and thus introducing a trinomial system.

What the author wishes to convey in a word to the reader is the general form of the corallum which he is about to describe so that a mental picture may be formed of the manner of growth of the coral the details of which will be learnt in the text. To those who have studied the genus at all the old specific names as a general rule convey to their minds this feature and this feature only, and it is consequently of value to retain some or all of these names as the one-word description of the form of growth. Instead of repeating therefore at the beginning of the description of each specimen the words "Millepora alcicornis" of the form of growth

attributed to Millepora species by authors," I propose to abbreviate it in each case thus, "Millepora alcicornis Facies 'x,'" or simply "Facies x," where "Millepora alcicornis" is understood.

The word "Facies" as it will be used will not convey more than the word "Colour" does in the description of species.

When we speak of a horse of black colour no one assumes that we mean a horse belonging to a black coloured species, and similarly when I use the expression "a Coral of dichotomous facies" or of "facies dichotoma" I do not mean more than that the particular specimen described happens to be of this form of growth.

#### MILLEPORA ALCICORNIS.

#### FACIES dichetoma.

There are several pieces of corallum which under the old system would have been included in the species *Millepora dichotoma* (Forskal).

Forskal's original definition of this species is as follows, "retiformis, laeviuscula, ramis teretibus, subcompressis, apice obtusissimis, poris minutis," and he adds in the more detailed description that the colour is "flavicans" and the habitat "profundum."

Forskal's specimens, like those described later by Klunzinger, came from the Red Sea.

The specimen collected by Dr Willey, from which the photograph (Fig. 1) was taken, is 15 centimetres in height and spreads out in one plane to a width of about 18 centimetres. The branches are slightly compressed and in the centre of the mesh reach a thickness of about 7 mm.

The degree of fusion in the branches is very variable. In one place, seen to the left of the centre in the figure, the branches have fused to form a plate 3 centimetres in breadth. In other specimens plates larger than this may be seen.

The surface of the corallum is generally smooth, but near the base of the "live'" corallum several irregular protuberances may be seen. These protuberances are due to the irritation caused by the growth of parasitic Algae<sup>2</sup> and worms.

These Algae are very common on the specimens, attacking not only the basal parts but in some cases the growing points. In one fragment a distinct spherical gall has been formed which can only be attributed to the effort made by the Millepore to surround and overwhelm the Alga which had attacked it. Parasitic cirripedes are rare on the Millepores of this facies, but as one fragment exhibits the characteristic key-hole aperture of Pyrgoma milleporae it cannot be said that they are free from the attacks of cirriped parasites.

The cycles of pores are on the whole well marked, but it will be noticed on

<sup>&</sup>lt;sup>1</sup> This term is used in its conventional sense and refers only to those parts of the corallum which were invested with living tissues when the specimen was killed by the collector. When a Millepore or a portion of a Millepore dies in its position on the reef the surface is attacked by parasites and sedentary creatures of various kinds and is thereby altered so materially that there can never be any doubt that it was dead if it be subsequently examined.

<sup>&</sup>lt;sup>2</sup> It is difficult to identify this Alga, but it appears to be closely related to Laurencia caespitosa Lamour. vel hybrida. Annal. Bot. v.

examining the figure with a lens that wherever there are ridges or other irregularities in the surface the gastropores are so crowded that the cycles become quite indistinct. Forskal says that the pores of this species are "minute." Actual measurements of twenty gastropores situated in the middle parts of the corallum give an average diameter of 0.28 mm. This average is above the average size of the diameters of gastropores in other specimens of Millepora (see list of average diameters of gastropores given in my paper in *Proc. Zool. Soc.*), and consequently it would be erroneous to state that in these specimens the pores are "minute."

The base from which the specimens of this facies spring is, in all cases which I have examined, either narrow or small. The base which supports the whole of the corallum shown in Fig. 1 is only 30 mm. by 10 mm. This is a point of some importance because the character of the ground on which the Millepore embryo settles must to a considerable extent determine its facies. It is quite certain that an embryo settling on a base only 300 square millimetres in area could never give rise to great plates of corallum similar to the one shown in the photograph Fig. 7. The colour of most of the specimens included in this facies is pale yellow brown.

#### Facies complanata.

Several specific names have been given to Millepores which assume the form of a broad leaf or a series of lamellae more or less coalescent. The descriptions given in the literature of the so-called species and of specimens attributed to species are so bewildering that it has become quite impossible to distinguish what form of growth is to be attributed to M. complanata Lamk., M. plicata Esp., M. platyphylla Ehr., and M. foliata, etc.

It will be convenient to consider those Millepores which form by coalescence broad lamellae under the name 'complanata.' These forms are practically those included by Pallas in his variety  $\gamma$ , with the following definition:

"Elegantissima omnium varietas quae effingitur in laminas latas, crassiusculas longitudinalibus plicis undulatis, sublaciniosas margine terminali retiusculo. Hae laminae in rupibus passim congestae, plerumque subparallelo positu; interdum tamen situ variantes imo decussantes aliquae reperiuntur."

The photographs given in Figs. 2 and 3 are the two halves of one specimen which shows admirably the manner in which the Millepores of this facies are formed.

The specimen began life on a broad frond of dead coral 14 centimetres broad and about one centimetre thick at the margin. (In this case the dead coral which forms the support is a Millepore covered by encrusting algae, foraminifera, zoantharian corals, etc.) At first the young Millepore spread as a thin crust over the support forming a broad base. At the same time a certain number of broad digitiform processes grew out from the middle of the base, which became broader and began to coalesce. If the process had been continued a little further, the lines of the original processes would have been obscured and a plate similar to that shown in Fig. 4 would have been formed.

The specimen shown in Figs. 2 and 3 is only one of several in Dr Willey's collection which give us information as to the mode of origin of the Millepore

colony, but it is the best for showing the intermediate stage between the branching form and the lamellar form which the colonies so frequently assume when growth has proceeded further. I have very carefully compared this specimen with the one shown in Figure 4 and with several specimens of the facies dichotoma, young and old. Neither the texture, size of the pores, average number of dactylopores to each gastropore nor any other feature indicates that we have here more than one species. A fragment of the specimen in Figure 2 cannot be distinguished by any characters from a fragment of the same size taken from the specimen shown in Fig. 4 nor from a specimen of the facies dichotoma unless it be a slight difference in colour or the number and size of tubercular processes on the surface.

Fig. 5 is a photograph of a specimen which under the old system would have been included in the species M. nodosa Esp. which closely resembles in form, as pointed out by Moseley (I.), Milne Edwards's M. gonagra vel M. tuberculosa.

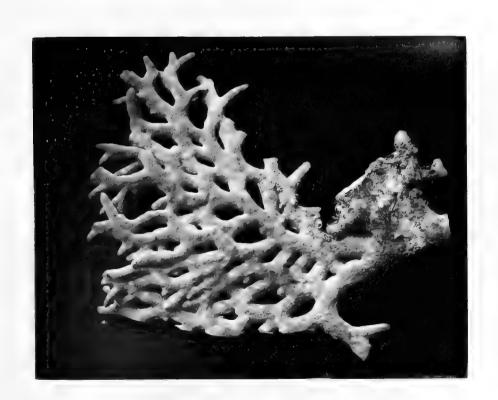
Moseley thought that a good character of this species is that the pores are distributed over the surface in well-marked systems. I cannot agree with this conclusion because in the two specimens in this collection the degree of definition of the systems varies enormously. An examination of Fig. 5 with a magnifying glass shows that in the lower half of the specimen the systems are very well marked, whereas in the upper half and at the edge the pores seem to be distributed indiscriminately. A better example of the variability of this feature in Millepora may be seen in Fig. 3 where the systems are perfectly distinct on the flat surface of the corallum but completely fused on the tubercles and at the edges.

#### SPECIMEN OF IRREGULAR FACIES.

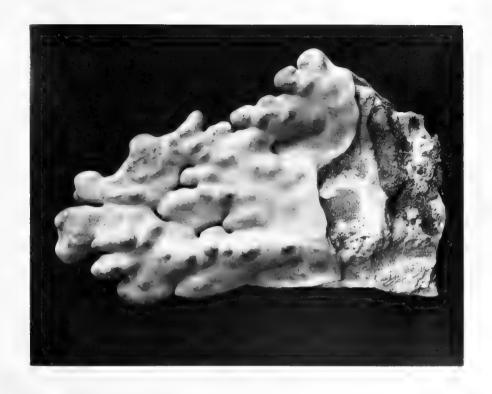
The large specimen of which a photograph is given in Fig. 7, presents us with so many different forms of growth that if pieces of it were judiciously broken off they might under the old system be placed in at least three different species. The upright flattened plate to the left in the figure with a relatively smooth flat surface would be included in the species M. complanata; the tuberculate knob on the right corresponds fairly well with the descriptions of M. gonagra v. tuberculosa of Milne Edwards; while the central parts might be considered to belong to the species M. verrucosa. Two important factors have brought about the irregularity of this specimen.

In the first place the specimen to a certain extent assumed the shape of an irregular lump of coral conglomerate on which it grew. During the transmission of the specimen the crust of live coral on one of the most prominent knobs was broken off and reveals an underlying knob of dead coral. This is shown in the photograph Fig. 6. This protuberance then which would have looked perfectly natural in the unbroken fragment was due not to any intrinsic tendency of growth of the species but to the chance form of the lump on which the individual specimen happened to be growing.

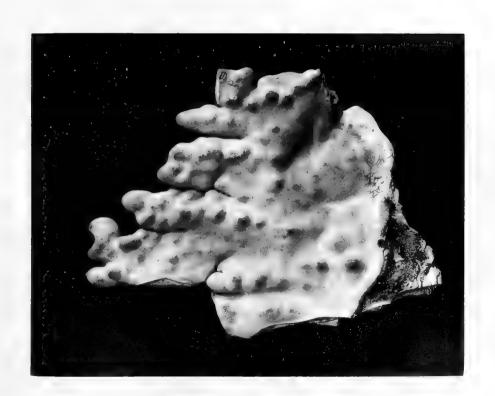
In the second place the irregular warty or tuberculate surface of the corallum is largely due to the influences of parasitic barnacles.



 $F_{Es.}$  1 MILLEPORA



Frs. 2. MILLEPORA.



 $F_{L}$ , 3 MILLEPORA



Fr. 4 MILLEPORA.

It will be noticed that at the summit of some of the tubercles there is a keyhole aperture, considerably larger in diameter than the gastropores, which is surrounded by one or in some cases two ill-defined circular grooves. These marks indicate the presence of *Pyrgoma milleporae* just below the surface and there can be little doubt that the irritation caused by the growth of the cirripede gave rise to hypertrophy of the coenosarc and produced the tubercle. In many cases however tubercles are present which have no cirripede holes at their summits, but the following considerations prove that the tubercles are nevertheless the results of parasitic irritation. A number of tubercles showing no external signs of the parasite were filed down to a level with the surface of the corallum or deeper, and others were fractured vertically with a bone forceps. In half of these an irregular cavity was found containing the remains of cirripede shells; in the remaining half no such cavity or remains were found.

The apparent absence of the cirripede remains may be due to incomplete examination, i.e. they may have been deeper down than I was able to get by filing from the surface, or the parasite may have been completely destroyed by the parasitic fungus Achlya, and the hole subsequently filled up with fresh corallum. The fact that in a large number of cases the tubercles are associated or were associated with parasites suggests that the tuberculate surface cannot be an intrinsic specific character, and this is confirmed by the fact that in the W.-Indian Millepores and in the Millepores from water 5—7 fathoms in depth parasitic cirripedes are rarely found and the surface of these corals is nearly always smooth.

#### Facies verrucosa.

I have given a figure of the largest and finest specimen in Dr Willey's collection as it forms a fitting termination to the series which has been described. If we were only acquainted with Millepores similar to the one figured in Fig. 8 and the one figured in Fig. 1, it would never have occurred to anyone that *M. verrucosa* and *M. dichotoma* were not good species. Yet the evidence which has been accumulating for the past ten years appears to me to prove that they ought not to be considered even as "varieties" of the one species. I believe that sister larvae might produce forms as widely different as these if they happened to settle on parts of the reef where the conditions of tide, bottom, food, parasites etc. were widely different.

The particular specimen is characterised by a surface covered with numerous tubercles of approximately the same size and shape, the key-hole cirripede aperture may be seen on the summit of many of these tubercles but in the majority of them the cirripede has been overwhelmed. The base of this specimen (not shown in the figure) which was broken across exhibits splendidly the dead cirripede shells corresponding with the tubercles. There is one more feature about this photograph which calls for notice. A broad meshed network of dark lines may be seen covering the corallum, running principally between the tubercles. These lines are marked by the deposit of a yellowish pigment, and I believe they represent the course of the principal and largest canals of the coenosarc such as those figured in Moseley's (I.) Plate XIV. Fig. 4 C, and in my woodcut 1, in Q. J. M. S., Vol. XXXII. The marking out of these canals is not easy to explain. I have only noticed it two or

three times among all the coralla I have examined, so that it is probably very rare. I am inclined to attribute it to the zooxanthellae which being present in large numbers in these canals have, in drying, stained the corallum. In coralla that have been slightly waterworn, I have occasionally seen this canal system marked out in grooves.

#### THE SPIRIT SPECIMENS.

Dr Willey sent me for examination a considerable number of specimens of different forms of growth carefully preserved in spirit.

I have decalcified large pieces and examined series of sections of specimens of dichotomous and of complanate forms of growth and of five different fragments from different localities. Unfortunately none of them show any signs of sexual organs.

I have found the medusae of Millepora in three collections only, namely that of Prof. Haddon from Torres Straits, of Mr Gardiner from Funafuti, and of Mr Duerden from Jamaica. My experience is that when the medusae occur at all they occur in great numbers. It is extremely probable therefore that further investigation of Dr Willey's specimens would not shew these organs.

The examination of the sections however has led to some interesting results in other directions.

In the first place I may say that the anatomy of gastrozooids, dactylozooids and coenosarc, and the size of the large and small nematocysts are the same exactly in the dichotomous forms as in the complanate forms. No specific differences can be drawn between the soft parts of these specimens, nor between the soft parts of these specimens and those from other parts of the world which I have examined. Two points of considerable interest in my sections of Dr Willey's material attracted my attention, namely, the condition of the nematocysts and the presence of a curious parasitic growth which has not hitherto been described.

NEMATOCYSTS. In my earlier investigations on the structure of Millepora it appeared to me that Moseley's account of the nematocysts of this genus was complete and accurate, but the discovery of a spiral fibril running up the lumen of the thread of the large nematocysts in some of the sections of Dr Willey's Millepores caused me to undertake their investigation with great care. The result is that while confirming the accuracy of Moseley's excellent observations in all essential details, I am able to add one or two points which have not been recorded.

As Agassiz originally pointed out, there are two kinds of nematocysts in Millepora which are usually referred to as the large and small nematocysts respectively.

The large nematocysts "never occur in the tentacles of the zooids, being confined to the coenosarc, and being present in greatest abundance in zonal masses around the bases of the zooids lying in the superficial layer of the ectoderm" (Moseley I.)

Regarding the small nematocysts Moseley says they are of a kind "which appears to be confined to Hydrozoa and not to occur at all in Anthozoa, viz. that in which a bladder-like enlargement of the thread occurs at that part of it which is immediately next the mouth of the cell, the bladder being armed near its summit by three spines set in one whorl. The three spines in this form of nematocyst in Millepora are remarkably long, and directed at right angles to the axis of the thread, instead of recurved, as is usual. These nematocysts vary very much in size.

The one figured is one of the largest observed, being two-thirds of the length of the ovoid nematocysts. The larger examples of these three-spined nematocysts are of comparatively rare occurrence, only a few being present in some of the tentacles and being more commonly present in the tentacles of the gastrozooids. The smaller nematocysts of this form have not more than one-sixth the length of the large ones."

All of these points I have repeatedly observed. The large nematocysts in the sections of some of Dr Willey's specimens exhibit a condition which we may assume is one of incomplete extension, the vesicle containing a fibril spirally wound at the base, which is continuous with the spiral fibril running in the lumen of the thread (Pl. XVI. Fig. 2). All of these nematocysts are fixed in the ectoderm of the coenosarc.

On examining the surface of the corallum with a lens or in searching through the débris at the bottom of the bottle in which it was present, a certain amount of white fluffy material may be found which consists of a felt-work of fully exploded nematocysts. An examination of these with the microscope shows details similar to those described and figured by Moseley (Pl. XVI. Fig. 1, copied with slight modifications from Moseley), no spiral fibril in the vesicle and thread being visible with ordinary powers of the microscope. Now it must be noticed that in the former the nematocysts are in contact with living cells, and may themselves be considered to be alive. In the latter the nematocysts may have been shot and dead sometime before the specimen was preserved.

It might be assumed that the fibril which is shown in Figure 2, drawn from a nematocyst fixed in the ectoderm, is the terminal portion of the thread fixed in the act of passing along the lumen of the basal portion of the thread to complete the fully exploded nematocyst. Its form indicates however that it is much more plastic than the outer wall of the thread, and as it stains deeply in haematoxylin, which the wall of the thread does not do, it must have at least a slightly different chemical structure. Moreover the spiral axis is equally present in fully exploded threads (see below). The appearance that the fibril has in the thread is strikingly like that of the myophan thread in the stalk of Vorticella, as Dr Willey remarks. These notes on the structure of the nematocyst of Millepora have some significance when taken in conjunction with the statement made by Dr Willey that the threads are retractile. In a private letter to me he says, "I think there can be no doubt now about the retractility of these threads. I did not observe it once or twice, but repeatedly in different stocks of Millepora. The retraction takes place suddenly just like a Vorticella." The retraction of these threads was observed with a lens, and it was particularly noticed that they were confined to the coenosarc and had no relation to the dactylopores or gastropores.

These observations of Dr Willey's seemed to me of such importance that I felt it to be essential to examine again with very great care the thread of the fully exploded nematocyst to see if it exhibited any traces of the spiral fibril. For this purpose I collected some of the felt-like substances from the surface of a colony, stained it deeply in Kleinenberg's haematoxylin, and examined teased preparations of it with Zeiss's 2 mm. oil immersion lens.

The result of this observation was to prove that in many of the fully exploded nematocysts a faint spiral line runs through the whole length of the thread. Considering the fact that some of the nematocysts collected in this way may have been shot a long time before they were preserved it is not surprising that some of the threads do not stain at all, but the observed facts are quite consistent with the view that a myophan fibril does run the whole length of the large nematocyst thread in Millepora.

I may point out in this place that the figure given by Moseley (II) of the large nematocyst of Cerianthus bathymetricus shows a fibril running up the lumen of the thread very similar to that which I have drawn in Fig. 2, but I can find no statement in this paper or in others which I have consulted as to the retraction of the thread.

Schulze, Allman and others have described fine processes proceeding from the base of the cnidoblast towards the deeper parts of the ectoderm, which Claus, Chun and Hamann considered to be probably muscular in function.

Thinking that the retractility of the nematocyst observed by Dr Willey might possibly be due to the chidopod, as Allman calls these processes, drawing back the whole nematocyst, I examined the sections of the best preserved material in my possession again very carefully to see if such processes occur in connection with the chidoblast in Millepora and arrived at the following conclusions. The nematocyst is enclosed in a chidoblast provided with an oval nucleus. Pseudopodial processes of the protoplasm often occur penetrating between the walls of neighbouring cells. These processes do not differ in structure from other parts of the protoplasm of the chidoblast and are consequently not specialised myophan strands (Pl. XVI. Fig. 5). The nematocysts may occur either in the ectoderm or in the endoderm, and probably migrate from the deeper parts of the canal system to the surface according to the needs of the colony. There is no chidocil, and the nematocysts may be exploded before they reach the surface (Pl. XVI. Fig. 4).

Moseley originally pointed out that the large ovoid nematocysts occur in the canal system in positions at a considerable depth from the surface, but apparently thought that they were always in the ectoderm. The thin sections which we can now prepare in great numbers have convinced me that they also occur in the endoderm, and in all probability migrate to the surface when necessary. The fact that in some of my sections a large number of exploded nematocysts are found at a considerable depth from the surface is of importance as proving that nematocysts are not always exploded by the trigger action of a cnidocil. In these cases the explosion must be due to a stimulus brought from a distance by the nervous system and not to a direct irritation of the cnidoblast.

Size of the Nematocysts. The vesicle of the large nematocysts is in all cases approximately '02 mm, in length. In every specimen there will be found slight

<sup>&</sup>lt;sup>1</sup> I have not thought it necessary to discuss more fully these points in the anatomy of the cnidoblasts, as the reader may find a full statement of the views on the subject in Allmann's Challenger Report on the Hydroida II. pp. xiv—xvii, and in the more recent paper of von Lendenfeld, "Die Nesselzellen der Cnidaria." Biol. Centralbl. xvII. July 1897.



Fr. 5 MILLEPORA.



Fi b MILLEPORA.



variations in this measurement, due I believe to the fact that some of them are, when killed, slightly more oval than others, but on taking the average of a large number of measurements the length is found to vary very slightly indeed from 02 mm. The small kind of nematocyst varies much more in size than the large kind. The largest of them which I found in the tentacle of a gastrozooid (Pl. XVI. Fig. 6), was 02 mm. from the whorl of spines to the base of the vesicle. The length of the vesicle before explosion must have been about two-thirds of this measurement.

PARASITE. In two of the spirit specimens, one a foliate form from Sandal bay and the other a plicate form, I noticed numerous white spots scattered over the surface of the coral having the general appearance of a rash. On decalcifying a portion of the specimen these spots were found to be quite irregular in form and varying in size from minute dots to lumps half a millimetre or more in length. It occurred to me that these bodies might be connected with the well-known parasitic fungus Achlya penetrans, the mycelial threads of which are almost invariably found in the deeper parts of the skeleton of Millepora. I have not yet detected these threads in the living superficial layer of any Millepore I have examined, but Moseley (I.) says, "They are not confined to the calcareous structure, but in Millepora nodosa (from Tahiti) at least occur also in abundance in the soft superficial tissues."

These bodies however are not apparently connected with the mycelial fibres, and their microscopic structure does not suggest that they belong in any way to a filamentous fungus. Each of the white bodies which can be seen on the surface by macroscopic observation is seen in section to be composed of a number of irregular lumps (Pl. XVI. Fig. 7). These lumps are so irregular in form and size that it is extremely probable they are due to shrinkage during preservation and of no morphological importance. Each lump consists of numerous minute lancet-shaped rods '004 mm. in length, arranged with their longer axes parallel. No trace of a membrane or wall enclosing the bodies as a whole or the lumps into which they are broken up can be found, and most of the bodies are completely isolated from their neighbours by normal healthy millepore tissues in which none of the rods can be traced. These rods readily stain in Haematoxylin, Borax-Carmine and Safranin, and when teased out on a cover-slip, separate in rows rather than in strings, as shown in the figure (Pl. XVI. Fig. 8).

The conclusion seems to be then that these bodies are clusters or zoogloeae of parasitic bacteria which may provisionally be called *Bacterium milleporae*. I cannot call to mind in the literature of the subject any previous note on the occurrence of bacteria in corals, and I can find nothing similar to these bodies in any of the preparations I have made of millepores and other hydrocorallines from other parts of the world. (Cf. Duncan.)

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## EXPLANATION OF PLATES XII.—XVI.

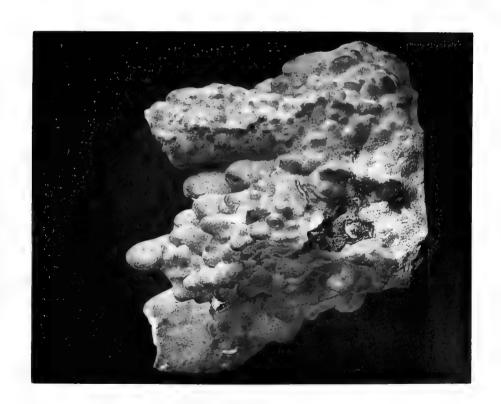
#### PLATES XII.—XV.

A series of Woodburytype reproductions of photographs of *Millepora alcicornis* taken by Mr J. T. Wadsworth,

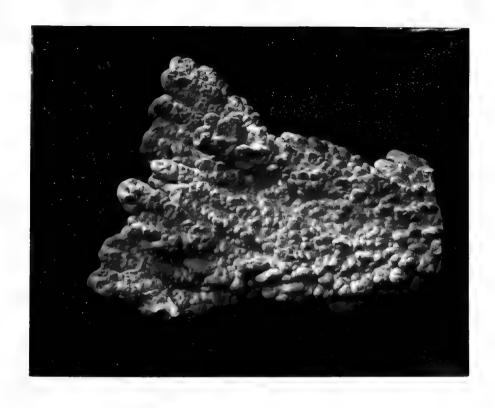
- Fig. 1. A specimen of the facies 'dichotoma,' ½ natural size. Some of the pores in this and the following figures show a white central spot like a columella. This is an effect of light and does not represent any actual structure.
- Figs. 2 and 3. Two pieces of a young form of the facies 'complanata,' \( \frac{3}{4} \) natural size. Both of these photographs show the pore systems well-marked and distinct on the general smooth surface but confused at the edges and on the summits of the tubercles. The manner in which the young Millepore encrusts a dead coral is well shown in fig. 2.
- Fig. 4. A piece of a large lamella belonging to the facies 'complanata,' ½ natural size. The surface of this piece is generally smooth, but two rounded prominences marked by the cirripede hole may be seen.
- Fig. 5. A specimen belonging to the facies 'complanata' covering a dead piece of coral, a natural size.
- Figs. 6 and 7. A specimen of very irregular facies.
- Fig. 6. \(\frac{3}{4}\) natural size, taken to show in the middle a knob from which the live coral has been broken off, revealing the dead coral on which it has grown, and which has given it the character of its form,
- Fig. 7.  $\frac{2}{5}$  natural size, showing the whole specimen. To the left a portion of the whole is of the form of growth described by authors as M. complanata, in the middle that described as M. vertucosa, and to the right that of M. nodosa. The summits of several of the tubercles are marked by cirripede holes.
- Fig. 8. A specimen of the facies 'verrucosa,' 1 natural size.

#### PLATE XVI.

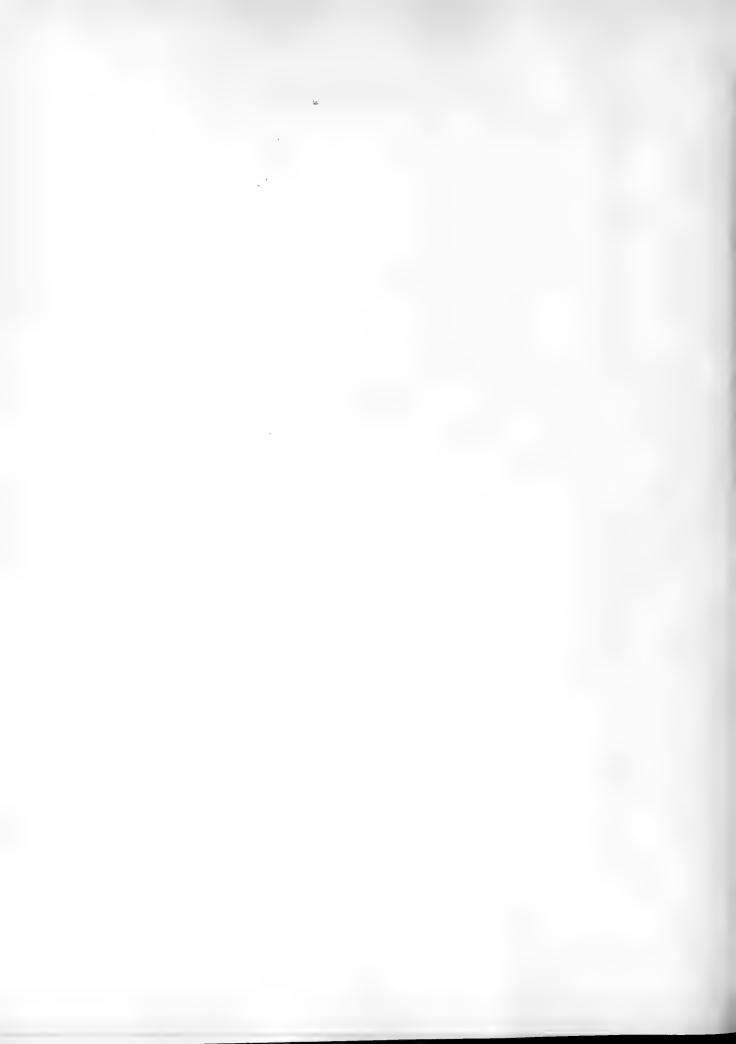
- Fig. 1. Large nematocyst of Millepora, the outline copied from Moseley. In the thread a thin spiral fibril may be seen in many specimens. The mode of attachment of this fibril to the cyst wall is uncertain.
- Fig. 2. Large nematocyst drawn with the assistance of the Camera lucida from a section of one of Dr Willey's millepores, showing a spiral fibril running through the thread distally and proximally coiled in the cyst.
- Fig. 3. A portion of that part of the thread of the large nematocyst which is beset with spirally arranged rows of thorns. In this part of the thread the spiral fibril drawn in Fig. 2 cannot be clearly traced but it appears again in the portion of the thread beyond the thorny part.
- Fig. 4. Drawn from a section of a millepore given to me by Professor Haddon. Shows a large exploded nematocyst deeply seated in the tissues below the Ectoderm. *Ect.* Ectoderm, *End.* Endoderm, *z.* zooxanthella.
- Fig. 5. An unexploded nematocyst in its chidoblast drawn from a section of the same material as fig. 4. n. nucleus of the chidoblast, ps. a pseudopodium of the chidoblast. Details of the thread coiled up in the cyst are omitted.
- Fig. 6. One of the small kind of Millepore nematocyst. Outline drawn with camera from a section of a gastrozoid tentacle in Dr Willey's material.
- Fig. 7. Outline sketch of canal system as seen in vertical sections showing the manner in which the Bacterium milleporae (bact.) occurs in zoogloeae, at the surface and in the canals.
- Fig. 8. The Bacterium milleporae as seen by Zeiss's 2 mm. oil imm.



F. 7 MILLEPORA



FL 8 MII LEPORA





# REPORT ON THE ECHINODERMS (OTHER THAN HOLO-THURIANS) COLLECTED BY DR WILLEY.

By F. JEFFREY BELL, M.A. (OXON.),

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With Figures on Pl. XVII, and One Figure in the text.

Dr Willey's collection of Echinoderms having been made in the intertropical area of what Mr T. Lyman called the "Great Ocean" contains, as was to be expected, a large number of well-known and widely distributed species; but he has, I am glad to say, been successful in finding Prof. Studer's Astropyga elastica, though he has not been equally happy as regards Schleinitzia crenularis, which I should very much like to see. He has obtained also some very interesting early stages of various Echinoderms, which will be useful when the changes that occur in species receive the attention they deserve. One very remarkable Echinoid will be duly described in its proper systematic place, and a figure is given of a young starfish as to which I am quite unable to offer any suggestions.

#### CRINOIDEA.

#### 1. Antedon indica.

Comatula indica, E. A. Smith, Phil. Trans. vol. 168 (1879), p. 564. Antedon indica, P. H. Carpenter, Chall. Rep., Comatulae (1888), p. 225. Loc. Blanche Bay, New Britain.

The specimens described by Mr Smith came from Rodriguez, so the area of the species is largely increased.

## 2. Antedon tuberculata.

Antedon tuberculata, P. H. Carpenter, Chall. Rep., Comatulae (1888), p. 232. Loc. Fiji.

This species does not appear to have been found since the 'Challenger' dredged a single specimen near Kandavu in 1874. Like Carpenter, I can distinguish it from A. indica.

19

3. Actinometra typica.

Phanogenia typica, Lovén, Öfv. Vet. Akad. Förhandl. 1866, p. 231.

Actinometra typica, P. H. Carpenter, Notes Leyd, Mus. iii. (1881), p. 195.

Loc. New Britain.

The history of this species has been very fully given by P. H. Carpenter in the work referred to, in the 'Challenger' Reports and elsewhere.

4. Actinometra grandicalyx.

Actinometra grandicalyx, P. H. Carpenter, Journ. Linn. Soc. xvi. (1882), p. 520.

Loc. New Britain.

I am by no means certain of the identity of Dr Willey's specimen with this species; it should be pointed out that it was founded by P. H. Carpenter on a single specimen, which is in the Hamburg Museum, but I am unable to make any better suggestion.

5. Actinometra bennetti.

Alecto bennettii, Müller, MB. Ak. Berlin, 1841, p. 187.

Actinometra bennettii, Böhlsche, Arch. f. Nat. 1866, p. 90; P. H. Carpenter, Notes Leyd. Mus. iii. (1881), p. 212.

Loc. Loyalty Islands.

It is of interest to observe that the two specimens collected by Dr Willey came from the same Islands as the specimen described by Dr Böhlsche in 1866.

6. Actinometra parvicirra.

Alecto parvicirra, Muller, MB. Akad. Berlin, 1841, p. 185.

Actinometra parvicirra, P. H. Carpenter, Trans. Linn. Soc. (1879), p. 27, and Chall. Rep. Comat. (1888), p. 338.

Loc. Sandal Bay, Lifu.

Dr Herbert Carpenter has dealt so fully with this species, which is widely distributed in the intertropical area, that there is nothing of importance for me to add.

# ECHINOIDEA.

7. Cidaris metularia.

Cidarites metularia, Lamk., An. s. Vert. iii. (1816), p. 56.

Cidaris metularia, de Bl., Actinol. (1830), p. 232; A. Ag. Rev. Ech. (1872), p. 385, Loc. Loyalty Islands.

This is another species of very extensive distribution.

8. Phyllacanthus annulifera.

Cidarites annulifera, Lamk., An. s. Vert. iii. (1816), p. 57.

Phyllacanthus annulifera, A. Ag., Rev. Ech. (1872), p. 387.

Loc. Milne Bay, New Guinea, 36 fms.; and New Britain.

Though with a somewhat extended area this species is comparatively rare. The spines, when fresh, were seen to be "quite covered with an incrusting Zoanthid."

# 9. Phyllacanthus gigantea.

Chondrocidaris gigantea, A. Ag. Bull. Mus. Comp. Zool. i. (1863), p. 18.

Phyllacanthus gigantea, id. Rev. Ech. (1872), p. 390.

Loc. Lifu.

This is a very rare species, but as it has been found at either end of the intertropical area (Sandwich Islands and Mauritius) it may be expected to appear from time to time at intermediate localities.

# 10. Phyllacanthus imperialis.

Cidarites imperialis, Lamk. An. s. Vert. iii. (1816), p. 54.

Phyllacanthus imperialis, Brandt, Prodr. descr. Animal. (1835), p. 68; A. Ag. Rev. Ech. (1872), p. 391.

Loc. Lifu.

This again is not a common species, but is known from a wide area.

# 11. Astropyga elastica.

Astropyga elastica, Studer, MB. Ak. Berl. 1876, p. 464.

Loc. New Britain, 50-70 fms.

The two specimens collected serve to confirm the accuracy of Prof. Studer's observations, but do nothing to increase our knowledge of the extent of the area which the species occupies. Dr Willey tells me that this form is commonly taken in the Nautilus baskets.

# 12. Astropyga radiata.

Cidaris radiata, Leske, Addit. Nat. Disp. Echin. (1778), p. 52.

Astropyga radiata, Gray, Ann. Phil. xxvi. (1825), p. 426.

Loc. Loyalty Islands; so far as I know this is a more westerly locality than has as yet been recorded for this species. One example is quite young, and will be useful in a study of the changes which the test undergoes during growth.

## 13. Mespilia globulus.

Echinus globulus, Linn. Syst. Nat. x. (1758), p. 664.

Mespilia globulus, Ag. and Des. Ann. Sci. Nat. vi. (1846), p. 358: Lovén, Bih. Svenska Vet. Akad. Hdlgr. xiii. (1887), iv. no. 5, p. 66.

Loc. Loyalty Islands.

## 14. Temnopleurus, juv.

Loc. New Britain.

## 15. Salmacis? sp. (pl. xvii. figs. 1 and 1a).

Dr Willey collected, at New Britain, a single specimen of a remarkable and interesting form, which is quite new to me, and has puzzled me a good deal.

The excellent figures which Mr Berjeau has drawn of it leave little for me to add, but I may point out that, though at first sight it appears to be a Cidaroid,

it is certainly a Triplechinid; the long solid spines, banded red and yellow, and the purple sinuous lines that mark out the interambulacra produces an elegant effect, which must be very marked during life.

I can only call attention to the form, and hope for a series of larger specimens. As it is suggested by the editor that it should have a name I propose to call it S. elegans.

16. Echinometra lucunter.

Echinus lucunter, Linn. Syst. Nat. x. (1758), p. 665.

Echinometra lucunter, Lütken, Videns. Meddel. 1863 (1864), p. 86; Lovén, Bih. Sv. Vet. Akad. Hdlgr. xiii. (1887), iv. no. 5, p. 157.

Loc. Cape Ventenat, Normanby Island, New Guinea.

17. Heterocentrotus trigonarius.

Echinus trigonarius, Lamk. An. s. Vert. iii. (1816), p. 51.

Heterocentrotus trigonarius, Brandt, Prodr. descr. Animal. (1835), p. 266; A. Ag. Rev. Ech. (1872), p. 430.

Loc. Loyalty Islands.

18. Arachnoides placenta.

Echinus placenta, Linn. Syst. Nat. x. (1758), p. 666.

Arachnoides placenta, Agass. Mon. Scutell, (1841), p. 94; Lovén, Bih. Svensk. Vet Akad. Hdlgr. xiii. iv. (1884), no. 5, p. 178.

Loc. New Britain.

#### ASTEROIDEA.

19. Astropecten monacanthus.

Astropecten monacanthus, Sladen, Chall. Rep., Aster. (1888), p. 216, ibique citt.

Loc. New Britain.

The 'type' of this species was collected by H.M.S. 'Challenger' off the Philippines. It would appear to be rare.

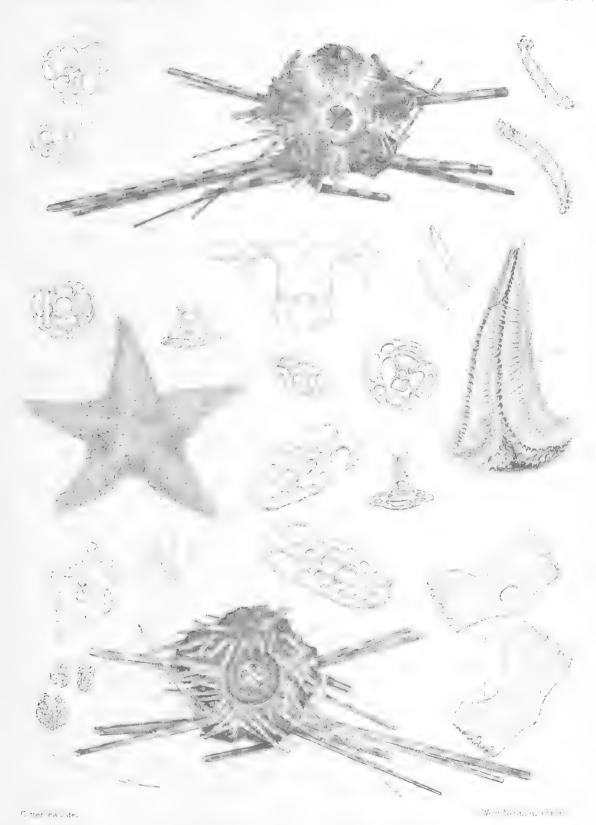
20. Pentaceros lincki, Loc. Blanche Bay. ) see Bell, P. Z. S. 1884, p. 72.

21. Pentaceros nodosus, id. t. c. p. 70.

These two species herd together in the narrow strait which divides the island of Matupi from the mainland. According to Dr Willey's observations the two species grade into one another both as regards colour and nodosity. He thinks they are either varieties of one species or else that they cross-breed together and produce hybrids.

22. Pentaceropsis obtusata.

Asterias obtusata, Bory de Saint Vincent, Encycl. Méthod. (1827), p. 140, pl. ciii.



BELL AND BEDFORD ECHINODERMA

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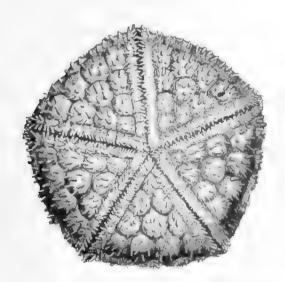
Pentaceropsis obtusata, Sladen, Chall. Rep., Aster. (1889), p. 351.

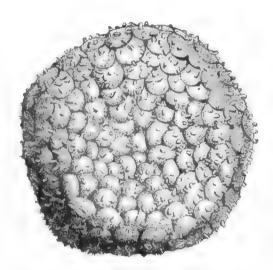
Loc. Blanche Bay.

Several specimens were obtained of this rare species. Mr Sladen indicates very briefly his reason for forming a new genus for the species, and the series at my disposal is too short to justify my supporting or declining to support his view.

### 23. Culcita.

A small specimen from Sandal Bay is of very great interest, as it is, so far as I know, the only example of its genus in which there is an imbrication of the plates of the dorsal surface (see fig.). The bearing of this on the affinity of *Culcita* to *Asterina* need not be insisted on.





Oral and aboral views of an undetermined specimen of Culcita from Sandal Bay, Lifu; showing imbrication of dermal plates on the dorsal surface. Diameter of specimen 13:5 mm.

## 24. Gymnasterias carinifera.

Asterias carinifera, Lamk., Anim. s. Vert. ii. (1816), p. 556.

Gymnasteria spinosa, Gray, Ann. and Mag. vi. (1840), p. 278.

Gymnasterias carinifera, Sladen, Chall. Rep., Aster. (1889), p. 357, ibique citata.

Loc. Lifu.

This is a species which appears to extend from the Red Sea to Panama, and is often found in collections from the Pacific.

## 25. Asterina exigua.

Asterias exigua, Lamk., Nat. Hist. s. Vert. ii. (1816), p. 554.

Asterina exigua, Sladen, Chall. Rep., Aster. (1889), p. 392, ibique citata.

Loc. Loyalty Islands.

This widely spread species was well represented.

W.

26. Fromia milleporella.

Asterias milleporella, Lamk., t. c., p. 564.

Fromia milleporella, Sladen, op. cit., p. 401, ibique citata.

Loc. Loyalty Islands.

27. Linckia multiforis.

Asterias multiforis, Lamk., t. c., p. 565.

Linckia multiforis, v. Martens, Arch. f. Nat., 1866, p. 65.

A very large number of this common and widely spread species were obtained at Lifu; common as it is, it is always of great interest from the manifold stages of budding that are to be observed, while often it exhibits exquisite galls, the result of the presence of *Stylifers*. It is needless for me to say anything more, where the Drs Sarasin have said so much, and have illustrated it so well (see Ergebn. naturw. Forsch. Ceylon, i. (1883), p. 73, pl. ix.).

28. Nardoa tuberculata.

Nardoa tuberculata, Gray, Ann. and Mag. vi. (1840), p. 287.

Loc. Sandal Bay; Loyalty Islands; Enganin Group, British New Guinea.

This is another species which was largely represented in the collection. Mr Sladen is in error in thinking he is the doer of 'a simple act of justice' in restoring Gray's name to this species; that was done, thirty years ago, by Prof. Verrill (see Trans. Connect. Acad. i. p. 285).

29. Acanthaster echinites.

Asterias echinites, Ellis and Solander, Nat. Hist. Zooph. (1786), pls. 60—62. Acanthaster echinites, Sladen, Chall. Rep., Aster. (1889), p. 537.

Loc. Loyalty Islands.

30. Mithrodia clavigera.

Asterias clavigera, Lamk., Hist. nat. An. s. Vert. ii. (1816), p. 562.

Mithrodia clavigera, Sladen, Chall. Rep., Aster. (1889), p. 539.

Loc. Loyalty Islands.

31. Echinaster purpureus.

Othilia purpurea, Ann. and Mag. vi. (1840), p. 282.

Echinaster purpureus, De Loriol, Mém. Soc. phys. Genève, xxix., no. 4 (1885), p. 10, ibique citata.

Loc. Off China Straits, British New Guinea.

This common species was very abundantly represented.

32. Echinaster eridanella.

Echinaster eridanella, M. Tr. Syst. Aster. (1842), p. 24.

As this species is already known from New Caledonia and New Ireland it is right it should be recorded from New Britain.

### OPHIUROIDEA.

The few Ophiuroids with two exceptions are common and widely distributed species; the exceptions are *Ophiomastix mixta*, which was collected in the Fijis by H.M.S. Challenger, and *Ophiomusium simplex*, which was first taken at Amboyna.

33. Ophiolepis annulosa.

Ophiura annulosa, Lamk., An. s. Vert. ii. (1816), p. 543.

Ophiolepis annulosa, M. Tr. Arch. f. Nat. 1840; Lyman, Chall. Rep., Ophiur. (1882), p. 19, ibique citata.

Loc. Blanche Bay, New Britain.

34. Ophiomusium simplex.

Ophiomusium simplex, Lyman, Bull. Mus. C. Z. v. (1878), p. 115; id. Chall. Rep., Ophiur. (1882), p. 93.

Loc. New Britain.

- 35. Ophiocoma erinaceus, M. Tr. Syst. Aster. (1842), p. 98.
- 36. Ophiocoma scolopendrina, Agass., Mém. Soc. Sci. Neuchatel, i. (1835).

Specimens of these two so-called species from China Straits, British New Guinea, revive the doubts raised by the late Dr Brock as to the advisability of keeping them separate (Zeits. f. wiss. Zool. xlvii. p. 495); it is certain that interbreeding experiments would give very interesting results.

37. Ophiocoma pica.

Ophiocoma pica, M. Tr. Syst. Ast. (1842), p. 101.

I do not remember finding this species associated with the two preceding before, but there is no cause for astonishment at the fact.

38. Ophiomastix annulosa.

Ophiura annulosa, Lamk., An. s. Vert. ii. (1816), p. 543.

Ophiomastix annulosa, M. Tr. Syst. Ast. (1842), p. 107.

Loc. Loyalty Islands.

39. Ophiomastix mixta.

Ophiomastix mixta, Lütken, Vid. Selsk. (5), viii. (1869), p. 99.

Loc. Sandal Bay, Lifu.

# DESCRIPTION OF FIGURES ON PLATE XVII'.

- Figs. 1,  $1^a$ . Salmacis elegans from the aboral, and oral poles.  $\times$  3.
- Figs. 2, 2a. Upper and under views (×2) of a Starfish, whose systematic position I am quite unable to determine, unless, indeed, it be allied to the Pythonasterinae of Mr Sladen. The single specimen is quite young, and it is possible that, later on, it would have lost the comparatively long spines that project from its dorsal surface; at this stage, at any rate, there is no sign of any nidamental pouch; the spines on either side of the ambulacral grooves are united by membrane into continuous fringes. This tantalizing specimen was collected at Sandal Bay, and it is to be hoped that larger examples with more definite characters will soon be obtained. It is hopeless to give it a name, as the editor suggests, as it is impossible to say in what genus it should be placed.

<sup>1</sup> Plate XVII faces page 150.

# HOLOTHURIANS.

BY F. P. BEDFORD, B.A. (CANTAB.).

With Figures on Plate XVII.

Owing to the kindness of Professor F. Jeffrey Bell I had the opportunity of working out the Holothurians in Dr Willey's collection, and I am much indebted to him for advice and assistance, and also for the use of the room which he kindly placed at my disposal at the Natural History Museum.

The collection comprises 24 species of which two, as far as I can discover, have not hitherto been described; of one of these there is unfortunately only one specimen, which is not in a sufficiently satisfactory state to render a complete description possible; of the other there are two specimens, and they seem to belong to a species which helps to bridge over the gap between Holothuria cinerascens and Holothuria moebii, and which I venture to call Holothuria willeyi. I also describe distinct local varieties, or topotypes, of Synapta ooplax and S. reticulata, both of which were represented by numerous specimens.

# I. FAMILY. SYNAPTIDAE.

1. Synapta ooplax v. Marenzeller, var. laevis nov. var. Fig. 3 a, b, c.

Reference: v. Marenzeller. Verh. Zool. bot. Ges. Wien, 1881, p. 4, Taf. iv. fig. 1. Loc. Sandal Bay, Lifu, Loyalty Islands.

Twenty-six specimens up to 15 cm. long; colour light reddish in spirit. They differ from the description given by v. Marenzeller in a few details; as far as I have observed, the holes of the anchor plates invariably have smooth margins with the exception that very rarely a pair of small teeth may be present, situated opposite to one another; the teeth figured and described by him as surrounding some of the holes do not seem to occur in this variety; biscuit-shaped spicules very common on the ambulacra, these occur only in the longitudinal radial muscles and not in the body-wall.

The Polian vesicles varied in number from 1 to 4 in the specimens dissected (about 6). In all other respects the specimens agree with those of v. Marenzeller.

2. Synapta beselii Jaeger.

Synapta agassizii Selenka. E. Selenka, Z. f. w. Z. 17, 1867, p. 361, Taf. xx.

References: C. Semper. Reisen Philipp. Hol. 1868, p. 11, Taf. i.

H. Ludwig. Z. f. w. Z. 35, 1881, p. 577.

H. Théel. Challenger Holothuroidea, 1885, p. 9.

K. Lampert. Die Seewalzen, 1885, p. 223.

Loc. Off China Straits, New Guinea.

Three fragments only, one of which was labelled as "striped" and distinctly answered to the description of var. agassizii, the other two were labelled as "spotted" when alive. Length of living specimens 60—64 cm. and upwards.

Lampert regards this form as a separate species; Semper has pointed out the similarity of colouring of S. beselii from different localities, and if not a true species the present form must be regarded as a well-marked colour-variety, although Mertens as quoted by Ludwig says of S. beselii "Die Farbe variirt wenn sie sich auch meist in denselben Farbentönen bewegt."

3. Synapta reticulata Semper, var. nigro-purpurea nov. var.

C. Semper. Reisen Philipp. Hol. p. 13, Taf. iv. figs. 4, 5.

References: C. Ph. Sluiter. Natuurk. Tijd. v. Ned. Indie, Bd. 47, 1887, pp. 214—215. K. Lampert. Zool. Jahrb. Systematik, Bd. IV. 1889, p. 845.

Loc. Isle of Pines, New Caledonia, between tide-marks.

Fourteen specimens up to 13 cm. in length; colour "crimson-black" when alive.

They seem to be similar to Semper's specimens in all respects except colour and size of anchors and anchor-plates, which are '24 mm. and '18 mm. in length respectively.

Lampert describes three examples from the Mermaid Straits which also differ from the type in the absence of reticulate markings, and Sluiter describes a colour variety under the term var. maculata, so that the identity need not be doubted on these grounds. It seems possible that the coloration may be correlated with the habitat, since Sluiter found the type at a depth of 6—8 fathoms and var. maculata at low-water mark.

4. Synapta recta Semper.

C. Semper. Reisen Philipp. Hol. 1868, p. 14, Taf. iv. figs. 2, 3.

Loc. Off China Straits, New Guinea.

One specimen 4 cm. long; tentacles up to 12 mm. in length; colour "speckled" when alive.

Corresponds exactly to Semper's description and figures. In fresh condition, 13 tentacles were counted. The colour consists of alternate light and dark greyish longitudinal bands, thickly speckled with whitish spots.

5. Synapta vittata Forskal.

References: J. Müller. Arch. f. anat. u. phys. 1850, pp. 132-134. S. serpentina.

F. Held. Vierteljahrsch. d. Nat. Gesell. in Zürich, 1857, pp. 264—266. S. vittata and S. raynaldi.

References: C. Semper. Reisen Philipp. Hol. 1868, pp. 11, 12, Taf. iv. figs. 6, 7, 8. S. grisea and S. glabra.

C. Ph. Sluiter. Semon's Forsch. in Austr. u. Mal. Arch. Bd. 5, Lf. 1. S. serpentina and S. glabra.

Loc. Off China Straits, New Guinea.

Only the anterior end of one specimen, the colour of which when alive was mottled yellow and black, giving an irregularly reticulate pattern. Length about 50 cm. Fifteen tentacles with numerous (about 30) pinnae, two black spots at inner base of each tentacle; anchors, anchor-plates, and miliary granules like those of S. glabra and S. grisea figured by Semper and those of S. raynaldi figured by Held; they are 29 mm. and 26 mm. in length respectively. Cartilaginous ring present; calcareous ring with short ascending processes; Polian vesicles numerous; gonads equal, a pair of wide tubes with numerous diverticula. There is some doubt as to how far this species is distinct from S. serpentina. The calcareous deposits of the specimen examined resemble what has been described for the latter, but there is said to be no cartilaginous ring in S. serpentina.

# 6. Chirodota rufescens Brandt.

Chirodota variabilis Semper. C. Semper. Reisen Philipp. Hol. 1868, pp. 20, 21. Taf. v. figs. 6, 7, 9—11, 19, &c.

Reference: H. Ludwig. Z. f. w. Z. 35, 1881, pp. 578, 579.

Loc. Loyalty Islands.

One specimen 9.7 cm. long, colour uniform reddish in spirit.

Seventeen tentacles; wheels of different sizes, all toothed; curved rods in body-wall confined to ambulacra; shorter rods occur in the radial longitudinal muscles; anatomy agrees with Ludwig's description of Brandt's original example.

Loc. Blanche Bay, New Britain.

Another specimen 6 cm.  $\log \times 1$  cm. broad, differs from the preceding in the absence of the red colour, in the transparency of the skin, and in the distribution of the curved rods over the interambulacra as well as the ambulacra; 17 tentacles, the pinnae of which appear to be retractile into a sheath at the base (cf. Mertens).

# 7. Chirodota rigida Semper.

C. Semper. Reisen Philipp. Hol. pp. 18, 19, Taf. iii. fig. 3, Taf. v. figs. 3, 13, &c.

Reference: H. Ludwig. Zool. Jahrb. Systematik, III. 1888, p. 819. C. amboinensis. Loc. Off China Straits, New Guinea.

A number of fragments including only one head; colour reddish-purple in spirit, with the wheel-papillae standing out as conspicuous white tubercles.

Tentacles, calcareous ring, deposits of body-wall, and colour correspond to Semper's description, but the pieces were too fragmentary to determine any further anatomical details; no C-shaped deposits, wheels up to 1 mm. in diameter, rods up to 07 mm. in length.

#### II. FAMILY. DENDROCHIROTAE.

1. Pseudocucumis africana Semper.

H. Ludwig. Zool. Jahrb. Syst. Bd. III. 1888, pp. 815-817.

Cucumaria africana Semper. C. Semper. Reisen Philipp. Hol. 1868, p. 53, Taf. xv. fig. 16 (since corrected by Ludwig).

Cucumaria assimilis Bell. F. J. Bell. Jour. Linn. Soc. xxi. 1886, p. 27, Pl. II. fig. 4.

Pseudocucumis théeli Ludwig. H. Ludwig. Sitz. Ak. d. Wiss. Berlin, 1887, Hft. ii. p. 1236. Taf. xv. figs. 12—16.

Reference: R. Koehler. Rev. Suisse de Zool. III. 1895, p. 277.

Loc. Isle of Pines, New Caledonia.

Three specimens 2.6 cm., 3.2 cm. and 4.5 cm. in length, of a uniform dark slate-colour.

A short historical account of this species is given by Prof. Koehler (l.c.). The tentacles were retracted in all three specimens collected so that their number and arrangement could not be made out. In all other respects the specimens agree with Ludwig's description of *P. théeli*, except that the "Kalkstäbchen" are confined to the feet themselves as in Semper's original example re-examined by Ludwig, l. c. 1888; the retractor muscles are inserted a short distance in front of the middle of the body as in Ludwig's specimens in which the tentacles were expanded, so that this condition does not seem to depend so much upon the state of retraction of the tentacles as upon individual variation.

- 2. Orcula (? Phyllophorus) dubia n. sp. Pl. XVII. Fig. 4.
- References: H. Ludwig. Arb. aus d. zool. zoot. Inst. in Würzb. II. 1875, p. 95.

  Orcula tenera.
  - H. Ludwig. Zool. Jahrb. Systematik, III. 1888, pp. 812—814. Taf. xxx. fig. 20. Orcula tenera and Phyllophorus brocki.
  - R. Koehler. Rev. Suisse de Zool, III. 1895, p. 278, fig. 2. Phyllophorus bedoti.

Loc. Lifu, Loyalty Islands.

One specimen, 10.5 cm. long; the description of this specimen is necessarily very incomplete. Owing to the complete contraction of the tentacles their arrangement could not be deciphered, but they appeared to number 15.

The only deposits that I can find outside the end-plates of the tube-feet are (1) "Hirseplättchen" like those described by Ludwig in *Phyllophorus brocki* and seen in a number of other Holothurians, and (2) occasional needle-shaped spicules of various sizes pointed at each end and often somewhat curved; both kinds are infrequent, the "Hirseplättchen" occurring loosely aggregated together. The calcareous ring has posterior bifurcate projections made up of a number of pieces on both radialia and interradialia, although only those attached to the former separate to form a definite arch as in *Phyllophorus bedoti* Koehler, and *Orcula tenera* Ludwig.

One Polian vesicle and one small stone-canal attached to the mesentery; gonads well developed, arranged like the fringe on a towel on each side of the mesentery.

<sup>&</sup>lt;sup>1</sup> These are minute crenulated nodules like a millet-seed.

## III. FAMILY, ASPIDOCHIROTAE.

- 1. Holothuria impatiens Forsk.
- H. botellus Selenka.

E. Selenka. Z. f. w. Z. 17, 1867, p. 335, Taf. xix. figs. 82-84.

C. Semper. Reisen Philipp. Hol. 1868, p. 82.

Loc. Lifu, Loyalty Islands.

Five specimens quite typical from 2 cm. to 6.4 cm. in length, tables .09 mm. diameter. In the smallest specimen the ventral feet are arranged quite distinctly in rows, buttons average about '09 mm. in length and are quite separate from the dorsal papillae,

2. Holothuria pardalis Sel. var. insignis Ludwig.

H. insignis Ludwig | H. Ludwig. Arb. a. d. Zool. Zoot. Inst. in Würz. Bd. 2,

1875, pp. 103, 105, 106, figs. 28, 30, 42. H. peregrina Ludwig)

? H. inhabilis Selenka. E. Selenka. Z. f. w. Z. 17, 1867, p. 333, Taf. xix. figs. 73-74.

References: C. Ph. Sluiter. Natuurk. Tijd. v. Ned. Ind. 47, 1887, p. 192.

H. Ludwig. Sitzb. k. Ak, d. Wiss. Berlin, 1887, p. 1226.

Loc. Reef off New Caledonia.

One specimen 3.6 cm. long; light grey in colour with violet-brown spots (cf. Sluiter); corresponds fairly to H. insignis Ludw., most of the buttons are somewhat arched, the central rib being often in a plane different from and parallel to that containing the sides and their surface is often uneven so that they approach the condition seen in H. inhabilis Sel. The resemblance of the button-like spicules of H. pardalis var. insignis to those of H. lentiqinosa von Marenzeller (Résultats des camp. scient. accomp. par Albert 1er Prince de Monaco, Fasc. VI. 1893) may be noted. The latter may possibly turn out to be a variety of H. pardalis.

3. Holothuria vagabunda Selenka. (Pl. XVII., Fig. 5 a, b, c.)

E. Selenka, tom. cit. p. 334, Taf. xix., figs. 75-76.

References: v. K. Lampert. Die Seewalzen, 1885, pp. 71, 242.

H. Théel. Challenger, Hol. 1885, pp. 180, 218.

R. Koehler. Mém. de la Soc. Zool. de France. T. VIII. 1895, p. 383.

Loc. Lifu, Loyalty Islands.

Two small specimens, 4.1 cm. and 2.2 cm. in length, belong to this species; the deposits agree with those described by Théel; discs of tables vary from '1 mm, to '04 mm, in diameter and spire varies in length considerably; the tables with small disc are provided as a rule with a short thick spire, while in the larger tables the spire is narrower and longer and very rarely more than one transverse bar can be seen; the crown nearly always carries 8 teeth and some of the small discs are uneven or even spinous on the margin; the deposits seem to approach those normally found in H. remollescens Lampert (fig. 5 a, b); the buttons, fig. 5 c, are occasionally

somewhat irregular. One large Polian vesicle. One fixed stone-canal. Cuvierian organs large and whitish in spirit. One of the specimens contained a *Eulima* (?) in buccal cavity.

Two more specimens from Lifu, Loyalty Islands, 10.5 cm. and 5.1 cm. in length, must also probably be referred to this species. The deposits differ in the fact that the tables do not vary much in size, the disc may be smooth, uneven or spinous, and the crown bears 10—12 teeth which are generally irregular. One of these specimens contained one very large Polian vesicle, one free stone-canal and Cuvierian organs; the other specimen had a *Eulima* attached to external surface, and was left unopened.

4. Holothuria decorata v. Marenzeller.

v. Marenzeller. Verh. Zool. bot. Ges. Wien, 1881, pp. 19, 21.

References: H. Ludwig. Notes from Leyden Museum, IV. 1882, p. 135.

H. Ludwig, XXII. Ber. d. oberh. Gesell. f. Nat. Giessen, 1883, p. 166.

K. Lampert. Zool. Jahrb. Syst. iv. 1889, p. 810.

Loc. Loyalty Islands.

One specimen, 13 mm. long, seems to agree fairly well with the original description; in colour it distinctly recalls H. monacaria from the same locality, a fact which lends support to Ludwig's hypothesis that H. decorata is the young of H. monacaria; the body-wall is thick (v. Ludwig, 1883, l.c.). Tables like those described, except that the disc is generally provided with at least 10 peripheral holes and often carries short spines; the longer spires may have as many as 5 transverse bars.

Buttons often uneven or arched (cf. *H. minax* Théel and *H. inhabilis* Sel.) and occasionally they have a finely granulated appearance (cf. *H. ludwigi* Lamp.); the distinction made by Ludwig between "Gitterplättchen" and "Schnallen" seems to be an arbitrary one, the one merging quite gradually into the other.

One Polian vesicle, one stone-canal, for greater part free, and terminating in an ovoid madreporite.

5. Holothuria monacaria Lesson.

References: K. Lampert. Die Seewalzen, 1885, p. 72.

H. Théel. Challenger, Hol. 1885, p. 172.

Loc. Lifu, Loyalty Islands.

Three specimens 4.5 cm., 10 cm. and 12 cm., in length.

In the smallest specimen a few of the discs of the tables bear short spines. The only specimen dissected had one Polian vesicle, one stone-canal free for about one-third of its length; in the two larger specimens the anterior end of the body is much thinner and more transparent than the rest (method of killing?).

6. Holothuria maculata Brandt.

Holothuria arenicola Semper. C. Semper. Reisen Philipp. Hol. 1868, p. 81.

References: H. Ludwig. Z. f. w. Z. 35, 1881, p. 595.

E. Hérouard. Arch. de Zool. Exp. Vol. I., 1893, p. 133, Pl. VII. B.

Loc. Several specimens from Lifu, Loyalty Islands, and one off China Straits, New Guinea.

Most quite typical, but in one of the Lifu specimens the spots are completely absent, and in the New Guinea specimen the spots are much darker and often confluent.

In three specimens dissected, several Polian vesicles and one stone-canal; deposits typical.

7. Holothuria atra Jaeg. var. amboinensis Semper.

H. Ludwig. Ber. Oberh. Gesell. 22, 1883, p. 170.

Holothuria amboinensis Semp. C. Semper. Reisen Philipp. Hol. 1868, p. 92. Holothuria atra Selenka.

E. Selenka. Z. f. w. Z. 17, 1867, p. 327. Taf. xviii. figs. 52, 53.

References: C. P. Sluiter. Natuurk. Tijd. v. Ned. Ind., 1887, p. 187.

K. Lampert. Zool. Jahrb. Syst. IV. 1889, p. 813.

C. P. Sluiter. Semon's Forsch. in Austr. u. Mal. Arch. Bd. 5, Lf. 1, 1894, p. 103.

Loc. Loyalty Islands.

Three specimens, 10 cm., 4.3 cm. and 3.7 cm. in length, all of the uniform black or dark-brown colour characteristic of var. amboinensis.

Deposits typical, discs of tables not always spinous.

TABLE OF VARIATIONS.

|       | No. of<br>free stone-canals<br>(in a group) | No. of<br>Polian vesicles | Cuvierian organs |
|-------|---|---------------------------|------------------|
| No. 1 | 8   | 1                         | Ş                |
| No. 2 | numerous                                    | 2                         | absent           |
| No. 3 | numerous                                    | 2                         | absent           |

Body-wall very much thicker in smaller specimen than in other two.

8. Holothuria edulis Lesson.

Holothuria fuscocinerea Selenka (not Jaeger).

E. Selenka. Z. f. w. Z. 17, 1867, p. 337, Taf. xix. fig. 36.

Reference: C. Semper. Reisen Philipp. Hol. 1868, p. 89.

Loc. Lifu.

One specimen 10 cm. long; colour in spirit dirty brown, darker on dorsal side.

Size of tables much more reduced than in H. atra.

Several Polian vesicles, about 14 stone-canals in a group, no Cuvierian organs.

9. Holothuria cinerascens Brandt,

Holothuria pulchella Selenka. E. Selenka. Z. f. w. Z. 17, 1867, p. 329, Taf. XVIII. figs. 61, 62.

References: C. Semper. Reisen Philipp. Hol. 1868, p. 89.

K. Lampert. Die Seewalzen, 1885, p. 82.

H. Ludwig. Z. f. w. Z. 35, 1881, p. 597.

Loc. New Caledonia.

Several specimens from 8 cm. up to 13.5 cm. in length.

The majority have a black ground colour on which the chestnut-coloured papillae and tube-feet stand out, each surrounded by a lighter space; in one specimen the brown colour is replaced by grey. Deposits quite typical.

|       | No. of<br>Polian vesicles | No. of<br>stone-canals free | Cuvierian organs     |
|-------|---------------------------|-----------------------------|----------------------|
| No. 1 | 4                         | 2                           | small                |
| No. 2 | 1                         | 3                           | none                 |
| No. 3 | 8                         | 2                           | moderately developed |

TABLE OF VARIATIONS.

10. Holothuria willeyi n. sp. Pl. XVII., Fig. 6 a, b, c.

Reference: v. H. Ludwig. 22 Ber. d. Oberh. Gesell. f. Nat. Giessen, 1883, p. 171. H. moebii, and also references to H. cinerascens.

Loc. Blanche Bay, New Britain.

Two specimens 2.2 cm. and 1.7 cm. in length in spirit; tentacles retracted; number?; colour in spirit light grey-brown with darker mottlings; tube-feet in 3 distinct rows on ventral surface; papillae(?) on dorsal surface much smaller and scattered; feet and papillae dark; deposits consist of tables and rods, besides the end-discs of the ventral feet. Tables are very infrequent; disc as in *H. cinerascens*, but spire reduced ending frequently in 3 or 4 points as in *H. pervicax*; the rods are of two kinds:—

- (1) curved granulated rods exactly like those of H. cinerascens up to 125 mm. long;
- (2) smooth rods unbranched up to 1 mm. long as in H. moebii. No H-shaped deposits.

Calcareous ring as figured (the top of the figure being posterior). One Polian vesicle; 6 stone-canals in a group; no Cuvierian organs.

The two specimens seem to agree in all respects and the species is undoubtedly allied to *Holothuria cinerascens* and *Holothuria moebii*; judging from the observations of Prof. Mitsukuri on *Stichopus japonicus* (Ann. Zool. Jap. Vol. 1, 1897) we might

regard *H. willeyi* as the possible young of *H. moebii*, from which it differs in the presence of tables and absence of H-shaped deposits, but it would be rash without further evidence to assume that the tables migrate during growth to the tube-feet and there become converted into the H-shaped supporting structures mentioned by Ludwig, just as the tables in *Stichopus japonicus* have been shown by Mitsukuri to become converted into the perforated plates of *Holothuria armata*, the two forms being merely different stages in the life history of a single species.

11. Holothuria difficilis Semper? C. Semper. Reisen Philipp. Hol. p. 92.

References: H. Ludwig. 22 Ber. d. Oberh. Gesell. Giessen, 1883, p. 173.

H. Théel. Challenger, Holothuroidea, 1885, pp. 219, 220.

H. Ludwig. Zool. Jahrb. Syst. III. 1888, p. 807.

Loc. Loyalty Islands.

One specimen 4 cm. long, colour whitish with dark violet blotches; I was at first inclined to refer this specimen to Actinopyga parvula; but I could not make certain of the existence of anal teeth; and the discs of the tables are better developed than in that form, the number of peripheral holes averaging about 25 in number and placed in 2 or 3 concentric circles; buttons generally with 8 holes, sometimes more, rarely fewer. 3 Polian vesicles, 1 small free stone-canal, Cuvierian organs large.

Seems to be more closely related to A. parvula than to H. vagabunda.

12. Actinopyga mauritiana Quoy and Gaimard.

Mülleria mauritiana. v. Selenka. Z. f. w. Z. 18, 1868, p. 116.

Mülleria varians Selenka. E. Selenka. Z. f. w. Z. 17, 1867, p. 310.

Taf. XVII. figs. 4—9.

Reference: K. Lampert. Zool, Jahrb. Syst. IV. 1889, p. 813.

Loc. Lifu, Loyalty Islands.

Several specimens from 3.5 cm. to 11 cm. in length; no distinct arrangement of ventral feet in rows although they are more closely situated in some places than in others; the colour seems to be very variable, the dorsal side is generally darker than the ventral, and there are nearly always indications of lighter spots surrounding the dorsal papillae.

The tentacles were in all cases retracted; in one specimen (the only one in which they were counted) they numbered 26. Deposits &c. quite typical.

13. Actinopyga lecanora Jaeger.

References: v. Semper. Reisen Philipp. Hol. 1868, pp. 75, 76, Taf. xxx. fig. 7. Ludwig. Z. f. w. Z. 35, 1881, pp. 592, 593.

Ludwig. Sitz. Ak. d. Wiss. Berlin, 1887. Hft. ii. p. 1223.

Loc. Loyalty Islands.

Two specimens, 20 cm. and 4.5 cm. in length. In the smaller specimen the ventral feet are in 3 quite distinct rows, the interambulacra being quite devoid of them, anal area lighter than rest of surface but not so conspicuously so as in the larger specimen.

14. Actinopyga maculata Brandt.

Mülleria nobilis Selenka. E. Selenka. Z. f. w. Z. 17, 1867, p. 313, Taf. xvii. figs. 13—15.

Reference: H. Ludwig. Z. f. w. Z. 35, 1881, p. 593.

Loc. Lifu.

One specimen 13 cm. long, calcareous ring not markedly conical, possibly referable to A. hadra Selenka.

15. Stichopus chloronotus Brandt. v. E. Selenka. Z. f. w. Z. 17, 1867, p. 315. Taf. xvII. figs. 20—24. Taf. xvIII. fig. 25.

References: H. Ludwig. Sitzb. k. Ak. d. Wiss. Berlin, No. 54 (1887), p. 1224. Taf. xv. fig. 4.

C. Ph. Sluiter. Natuurk. Tijd. v. Ned. Ind. (1887), Bd. 47, p. 195.

K. Lampert, Zool, Jahrb. Syst. Bd. iv. 1889, p. 815.

Loc. Lifu, Loyalty Islands.

Two specimens, 5.6 cm. and 8.1 cm. in length.

The larger specimen contained a *Fierasfer 8.2* cm. long, which Mr Boulenger has kindly identified for me as *F. homei* Richards. Rosette-shaped bodies as well as intermediate forms between these and the much more abundant C-shaped deposits occurred as figured by Ludwig; S-shaped deposits excessively rare.

## EXPLANATION OF FIGURES ON PLATE XVII.

- Fig. 3. Synapta ooplax.
  - a. anchor and anchor-plates.  $\times$  250.
  - b. biscuit-shaped ambulacral and rod-like interambulacral spicules. × 250.
  - c. radial and interradial pieces of calcareous ring. x 35.
- Fig. 4. Orcula (? Phyllophorus) dubia, n. sp. Spicules of body-wall. × 250.
- Fig. 5. Holothuria vagabunda, young.  $\alpha$ . smaller tables, b. larger tables, c. buttons.  $\times$  250.
- Fig. 6. Holothuria willeyi, n. sp. a. tables.  $\times$  250. b. rods.  $\times$  250. c. calcareous ring (post. end at top of figure).  $\times$  about 10.

# A REPORT ON THE SIPUNCULOIDEA, COLLECTED BY DR WILLEY AT THE LOYALTY ISLANDS AND NEW BRITAIN.

ВУ

# ARTHUR E. SHIPLEY, M.A.,

Fellow and Tutor of Christ's College, Cambridge, and University Lecturer on the Morphology of the Invertebrata.

## With Plate XVIII.

Dr Willey brought back with him from the Loyalty Islands and New Britain, twenty-three species of Sipunculoidea which are divided amongst the following genera: Aspidosiphon, Cloeosiphon, Phascolion, Phascolosoma, Physcosoma and Sipunculus. Six of his species were found by Mr J. Stanley Gardiner (X)<sup>1</sup> at Funafuti and at Rotuma, Mr Gardiner's collection contained seven species unrepresented in that of Dr Willey.

I have added brief notes on some of the more important features of the species catalogued and a list of the localities from which each has been recorded. An examination of the latter seems to extend the view that I expressed in 1891 (XI) as to the headquarters of the genus Phymosoma (now called Physcosoma) (IX). A further examination seems to show that not only are the headquarters of the last named genus in the Malay Archipelago, but that the seas which surround that group of islands and which stretch up the east coast of Asia as far as Japan and round the north and east of the great Australian continent, and throughout the South Pacific abound in species of Aspidosiphon, Cloeosiphon, Physcosoma and Sipunculus.

Several of Dr Willey's species occur elsewhere, some of them spread through the Indian Ocean and have been collected in the Red Sea and off Mauritius and the east coast of Africa, and several species are cosmopolitan. The genus Cloeosiphon is confined to the seas mentioned above, both it and Physcosoma, and possibly Aspidosiphon are usually found associated with coral-reefs, and this fact probably explains the paucity of their numbers in the eastern waters of both the Pacific and Atlantic Oceans. Physcosoma agassizii is however found along the West coast of both Americas from Esquimault to Puntarenas<sup>2</sup> and again at the Loyalty Islands.

<sup>1</sup> The Roman numerals in brackets refer to the literature at the end of the article. For some of the references I am indebted to Selenka's Monograph (viii.).

<sup>&</sup>lt;sup>2</sup> The place here referred to is on the Straits of Magellan. It is not sufficiently recognized that there are three places with this name on the Pacific Coast, besides one in Venezuela. A fact which once took an unfortunate Spaniard many thousands of miles out of his direct route.

The two largest collections of Sipunculoidea, that of Professor Semper, and that of Dr Sluiter, which have been worked out, were collected in the seas surrounding the Malay Archipelago and the Philippine Islands. This probably accounts for the fact that in Dr Willey's collections I have found no new species, and it must also be taken into account in assigning the headquarters of certain genera to these seas. But making due allowance for the fact that these seas have been more carefully searched than many other parts of the globe, it still seems to me that this region is the centre of the above-mentioned genera of Sipunculoidea.

Sipunculus priapuloides has a curious distribution, being found off the Norwegian coast, and again at the Loyalty Islands.

The determination of the species of a Sipunculid is not always an easy matter. Some are readily enough identified and the task is rendered easier if the animal dies with its head extended. But this is seldom the case and then it is not easy to make out the arrangement of the tentacular erown, the number of tentacles etc.

In those species which are provided with hooks the number of rings in which they are usually arranged and the shape of the hooks are of systematic value, but here again we are met with the difficulty that the hooks are often worn away with age and it is not possible to tell how many rings have disappeared. Further, the shape and size of the hooks are by no means constant, but vary considerably in the same species and even in the same specimen.

Again the number of longitudinal muscles in those species in which this muscular coat is split up into bundles is an important specific character, yet in many species the bundles anastomose to such an extent, that the number of bundles at any one level differs from that at any other. This fusing and splitting of the bundles also obscures the question of the exact origin of the retractor muscles.

Perhaps one of the most fruitful sources of difficulty is the difference of colour and the relative prominence of the papillae which is brought about by the varying states of contraction in which the animals die. The pigment of the skin is as a rule aggregated around the mouths of the papillae, and when the animal is killed in a contracted state, the colour is much deeper and the papillae far more prominent than when the skin is relaxed. Hence as in the case of Cloeosiphon aspergillum for example, specimens are met with whose appearance is so different that at first sight one is disposed to think that at least two distinct species exist, but a more minute observation tends to show that the superficial differences depend largely on the condition in which the creature died.

Species are a matter of opinion and few groups of animals afford so wide a range for divergency of opinion as do the Sipunculoidea.

It should be mentioned that all the specimens examined had been long in spirit and were killed with diverse reagents. This may to some extent account for the very different appearance and colour presented by some specimens of the same species.

### I. GENUS. ASPIDOSIPHON, Grube.

## 1. Aspidosiphon elegans Cham. and Eysenh. (I.)

Three specimens from Lifu, Loyalty Islands. This species was taken by Mr J. Stanley Gardiner at Funafuti, and is described in Selenka's Monograph (II) from the Pacific Ocean, the Philippines, and Koseir.

## 2. Aspidosiphon klunzingeri Sel. and Bülow. (VIII.)

One specimen, measuring 3 cms. from the posterior shield to the base of the introvert. The latter measured in a partially retracted condition 1.5 cm. The breadth of the body is 1 cm.

This species was described by Selenka and von Bülow from three specimens collected by Klunzinger at Koseir. I have described another specimen collected by Mr J. Stanley Gardiner at Funafuti, and as I know of no specimen being figured, I have added a sketch. (Fig. 1.) The species is also recorded by Dr W. Fischer¹ from Amboyna in the Moluccas.

### 3. Aspidosiphon ravus Sluiter. (XII.)

Several specimens of the interesting species were found at Sandal Bay, Lifu. As Sluiter gives no illustrations of the external appearance of this animal, I have added a couple of figures. I append a few notes which amplify the account we owe to the Dutch naturalist. The continuous sheet of longitudinal muscles breaks up anteriorly into a number of anastomosing bundles. Along the ventral middle line on each side of the nerve-cord the muscles of the skin were, in the specimen opened, very thin so that an attenuated transparent strip of integument marked the neural surface. (Fig. 2.) A similar strip was visible externally in some of the other specimens, but not in all. The nephridia were long and each was attached by a posterior muscle to the body-wall.

The most interesting feature in the species is the presence of numerous dark brown spines on the base of the proboscis, arranged in irregular rows. (Fig. 3.) Sluiter has figured one of these, they are not hooks but horny spines, and disappear at the level where the rows of hooks make their appearance.

# 4. Aspidosiphon steenstrupii Diesing. (II.)

Several specimens from Sandal Bay, Lifu, Loyalty Islands, some with their introverts fully expanded and their tentacles spread out. All the specimens were young and showed hardly any trace of calcification in the anterior shield.

A peculiarity of this species is that the cuticle very readily separates from the underlying skin, and often projects from the posterior end of the body for a length at least equal to that of the trunk. The cuticle is transparent and bears on it the outlines of the papillae and their pores.

<sup>&</sup>lt;sup>1</sup> Semon's Zoologische Forschungsreisen in Australien und den Malayischen Archipel, Bd. v., Lief. III, 1896, p. 338.

This species is also described from the Mauritius and the Philippines, and a specimen of what I take to be the same species was brought home by Professor Weldon from the Bahamas.

## 5. Aspidosiphon truncatus Keferstein. (III.)

Two specimens found in Sandal Bay, Loyalty Islands. This species is recorded from the Mauritius and from Panama.

### II. GENUS. CLOEOSIPHON, Quatrefages.

### 6. Cloeosiphon aspergillum Quatrefages. (VII.)

Numerous specimens, some imperfect, from Sandal Bay, Lifu, Loyalty Islands. This species is registered in Selenka's Monograph from Caminguin, Uhoy; Zamboango; Luzon; Mauritius; Ibo and the Viti Islands, and by Dr W. Fischer<sup>1</sup> from Thursday Island, Samoa, and off the East African coast.

An examination of the specimens brought home by Dr Willey affords a good example of the difficulties of systematic work amongst the Sipunculids. His specimens fall readily into two groups, one with a thin transparent skin, of a uniform gray colour, with no apparent papillae, the other of individuals with thick opaque skins. harsh to the touch and with papillae just visible to good eyesight. The members of this latter group are not always uniform in colour and are for the most part either deep yellow or brown. Here I thought are two distinct species. On opening the bodies of one of each group, although the relative size of the organs varied owing to the different states of contraction in which they had been when killed, I could detect no real differences of structure corresponding with the differences of the external appearance. I re-examined the skin with the aid of a lens and found that though few in number there were some papillae in the transparent specimens, chiefly at the posterior end but also round the base of the chalky ring. Finally I prepared specimens of the hooks on the introverts of members from each group; in colour, size and shape, the hooks exactly resembled one another. There thus seemed no doubt that these two groups although they differed externally to a very marked degree formed in reality but one species.

### III. GENUS. PHASCOLION, (Théel) Selenka and de Man.

### 7. Phascolion manceps Sel. and de Man. (VIII.)

One specimen only was found, and this was so small that I had considerable difficulty in making out the anatomical features. However, I have little doubt that this specimen belongs to the species *Phascolion manceps* which Selenka and de Man described from a single specimen taken in a Nassa shell in the Philippines (Uhoy). Dr Willey's example was living in the shell of a young Mollusc named *Astralium moniliferum* Hed. and Wil., which has been recently described<sup>2</sup>. The shell and its contents was taken in the trawl off Man Island, Talili Bay, New Britain, in 35 fathoms.

<sup>&</sup>lt;sup>1</sup> Loc. cit. p. 338.

<sup>&</sup>lt;sup>2</sup> P. Linn. Soc. N. S. Wales, Part 1., p. 107.

# IV. GENUS. PHASCOLOSOMA, (F. S. Leuckart) Selenka and de Man.

## 8. Phascolosoma pellucidum Keferstein. (IV.)

One specimen found at Lifu, Loyalty Islands. This species has a very wide distribution, being recorded in Selenka's Monograph from the West Indies, Rio de Janeiro, the Philippines, Singapore, and Torres Straits.

# V. GENUS. PHYSCOSOMA, Selenka.

## 9. Physcosoma agassızii Keferstein. (III.)

Four specimens from Lifu, Loyalty Islands. Keferstein<sup>1</sup> in a description of this species dwells on the variability of the external features and appearance of this animal, and figures three very different looking specimens of the species. The figure of the Panama specimen closely resembles two of the four individuals collected by Dr Willey, the other two from the Loyalty Islands had their introvert more retracted and more closely resembled another specimen figured by Keferstein who does not mention its place of origin.

The species has been found at numerous places along the western coast of America from Esquimault to Puntarenas. Fischer records it from Ambrizetta near the mouth of the Congo, and from Ponapé one of the Carolines.

## 10. Physcosoma asser Sel. and de Man. (VIII.)

Numerous specimens from Sandal Bay, Lifu, Loyalty Bay, and one specimen from New Britain.

This is one of the few species of Physcosoma which has no hooks, but the skittle shaped papillae on the short proboscis are capped by a thickened cuticular layer which only wants bending over on one side to form a hook.

In Selenka's Monograph it is described from Batjan, Sluiter found it at Billiton, and Fischer records it from Mozambique.

### 11. Physcosoma duplicigranulatum Sluiter. (XIII.)

Four specimens from Blanche Bay, New Britain.

The specimens corresponded fairly well with the species described by Sluiter from the Malay Archipelago except as regards the number of rows of teeth; but in this point they differed very materially inter se.

### 12. Physcosoma lacteum Sluiter (XIII.)

Two specimens from Lifu, Loyalty Islands. The species was founded by Sluiter on specimens collected in the Malay Archipelago. The specimens at my disposal agree with his description, but the remarkably wrinkled and parchment-like nature of the skin is not mentioned by him.

## 13. Physcosoma pacificum Keferstein. (III.)

Numerous specimens from Uvea, Loyalty Islands, and a single specimen—rather a small one—from Blanche Bay, New Britain.

The introvert was in every case retracted, and in this condition the length of the body reached a maximum of some 11 cm. Many specimens were however shorter. The species is widely distributed throughout the Indian and South Pacific Oceans.

### 14. Physcosoma scolops Sel. and de Man. (VIII.)

A few specimens from Sandal Bay, Lifu, Loyalty Islands.

The specimens were all small and apparently young forms. In the one I opened there was a curious abnormality in the nephridia. One was small and almost without pigment, but the other was large, dark brown and forked, the two branches being equal in size.

This species has been recorded from Koseir in the Red Sea, Singapore, the Philippines, and Amboyna in the Moluccas.

Fischer regards this species as a variety of *Physcosoma granulatum*, and if this is so, the species occurs on the East and West coasts of Africa, and in the Mediterranean and Adriatic Seas.

# 15. Physcosoma spengeli Sluiter. (XIII.)

Several specimens from Lifu, Loyalty Islands.

Sluiter gives the relative lengths of the diameters of the body, but does not mention the absolute length. Dr Willey's specimens varied much in size, the smaller being some 7—8 mm. long, the larger when fully stretched out, but not with the introvert everted, some 2.5 cms. All the specimens were somewhat bent, i.e., new moon shaped.

#### VI. GENUS. SIPUNCULUS, Linnaeus.

#### 16. Sipunculus australis Keferstein. (IV.)

Eight specimens from Lifu, Loyalty Islands.

Dr Willey's specimens measured from 5 cm. to 18 cm. or so, and were all of a dark almost purplish colour.

S. australis is described in the books as the only species of Sipunculus which bears hooks on the introvert. A closer examination of the cuticular structures of the introvert shows that they differ materially from the hooks of Physcosoma. Like them however they are cuticular, arranged in circles and bear a definite relation to the glandular bodies of the introvert. This relation is shown in the Figure 4. A transverse section (Fig. 5) shows that the relation of these cuticular structures to the underlying epidermis is similar to that of the Physcosoma hooks, but if isolated by boiling in caustic potash it is immediately apparent that their shape is different. Dr Johnson gives as the primary definition of a hook "Anything bent so as to catch hold": if

this definition still holds, the structures are not hooks. They are rather of the shape of a roll of paper so folded as to form a half cylinder rather rounded at both ends. Their presence serves to distinguish this species from others of the same genus, but they should no longer be termed "hooks."

This species is recorded in Selenka's Monograph, from Sydney, the Philippines, Fiji and Amboyna.

## 17. Sipunculus billitonensis Sluiter. (XIII.)

Numerous specimens from Lifu, Loyalty Islands.

Dr Willey's specimens were somewhat shorter than those described by Sluiter, none of them surpassed 18—20 cms. in length, but in other respects they correspond well with the description given of the type. As Sluiter has not figured the outside, I have done so (Fig. 6). The anus is very prominent, ridged and ribbed (Fig. 7).

### 18. Sipunculus cumanensis Keferstein. (III.)

Three specimens varying in length from 3.5 cm. to 12 cm. from Uvea, Loyalty Islands.

I am inclined to think that these specimens belong to the variety S. cumanensis opacus Sel. and Bülow, which is recorded from Mauritius and Ascension. The species is widely spread and has been found off Venezuela, and Ascension, in the Red Sea, off Mozambique and the Philippines.

The characteristic transverse dissepiments which stretch across the body on the inside of the skin were, in the specimen I opened, much more prominent in the posterior third of the body than in the anterior two-thirds. The numerous diverticula of the heart are very definitely arranged in two lateral rows.

Some specimens of the variety S. cumanensis vitreus Sel. and Bülow were gathered at Blanche Bay, New Britain, and one example at the Isle du Phare, Nouméa. The circular muscles of these specimens were very violently contracted, and gave the outline of some examples a very extraordinary appearance (Fig. 8). One of this variety attained a length of 20 cm.

#### 19. Sipunculus edulis Lamarck. (VI.)

Numerous specimens from Lifu, Loyalty Islands, and five from Gavutu near Florida, one of the Solomon Islands.

None of the specimens were, in the retracted state, longer than 12 cms., and were thus shorter than Sluiter's specimens from Reede Batavia, Tandjong Priok which measured 15 to 18 cms. (XII and XIII). But the Lifu specimens may have been young or the Malay specimens may have been extended.

The colour of the examples from Lifu was darker than Sluiter mentions and the circular muscles are divided into fine bundles, but in other respects the animals corresponded with his description. Dr Willey tells me that he thinks the specimens have darkened in spirit, and this is undoubtedly the case in some specimens of Balanoglossus—though not in all—that he brought home. The five examples from the Solomon

Islands retained their light straw colour, and the circular muscles do not show any sign of division into bundles, nevertheless I think the two sets of specimens belong to the same species.

This is the species eaten by the Chinese.

### 20. Sipunculus mundanus Sel. and Bülow. (VIII.)

Four specimens from Pigeon Island, New Britain.

The single specimen dredged on the Sow and Pigs Bank, in the British Museum, from which Selenka and Bülow established the species was 33—34 cms. long. Dr Willey's specimens were much shorter, the longest alone attaining a length of 10 cm. As the only specimen opened showed no trace of reproductive organs, it is probable that they are all young forms.

### 21. Sipunculus nudus L.

Two specimens from Blanche Bay. The posterior end of one of them had been seized by a small bivalve which had been partly dragged into the cavity formed by the introversion of this part of the body. This species is practically cosmopolitan, Selenka records it from the North Sea, English Channel, Mediterranean, Zamboango, Malacca, the West Indies and Florida.

## 22. Sipunculus priapuloides, Kor. and Dan. (V.)

One specimen from Lifu, Loyalty Islands.

This specimen agreed very well with the description of the species given by Koren and Danielssen, the portion of the body from which the specific name is taken is however not so prominent as in the figure of the animal given by the Norwegian artists. There is however a clear change in the external appearance of the skin at the posterior end. The specimen which had been two years in spirit was of an iridescent gray colour. Koren and Danielssen's specimens came from Korsfjord near Bergen and from Søndfjord, so that this species has a remarkable range.

## 23. Sipunculus vastus Sel. and Bülow. (VIII.)

Four specimens from Pigeon Island, New Britain; numerous specimens from Lifu, Loyalty Islands, and two from the Isle of Pines, New Caledonia.

This species was found by Mr Stanley Gardiner at both Rotuma and Funafuti and seem common. Selenka records it from the Marshall group of Islands. The Lifu examples were much darker in colour and more opaque than those from New Britain and from New Caledonia; in fact like the most nearly allied of its fellow species, S. cumanensis, it may be divided into at least two varieties, S. vastus albus which is a pearly white and fairly translucent and S. vastus obscurus which is a dark purplish brown and quite opaque.

THE ZOOLOGICAL LABORATORY, CAMBRIDGE.

August, 1898.

#### LIST OF LITERATURE.

The abbreviations here adopted are those suggested by Dr D. Sharp in the Zoological Record.

- I. Chamisso and Eysenhardt. De animalibus quibusdam e classe vermium lineana, etc. Acta Ac. Germ., T. x. Pt 2, 1821, p. 351.
- II. DIESING. Revision der Rhyngodeen. SB. Ges. Wien, Cl. 37, 1859, p. 767.
- III. Keferstein. Untersuchungen über einiger amerikanishe Sipunculiden. Nachr. Ges. Göttingen, Juni 13, 1866, and Zeitschr. wiss. Zool., Bd. xvii., 1866, p. 50.
- IV. KEFERSTEIN. Beiträge zur anatomischen und systematischen Kenntniss der Sipunculiden. Nachr. Ges. Göttingen, März, 1865, p. 204, and Zeitschr. wiss. Zool., Bd. xv., 1865, p. 433.
- V. Koren and Danielssen. Fauna Littoralis Norwegicae, Hft. III., 1877, p. 126.
- VI. LAMARCK. Animaux sans vertèbres. 1st Ed., Bd. III., 1816, p. 79; 2nd Ed., Bd. III., 1840, p. 469.
- VII. QUATREFAGES. Histoire naturelle des Annelés. T. II., 1865, p. 605.
- VIII. Selenka. Die Sipunculiden. Reisen in Archipel der Philippinen, Th. II., Bd. IV., Abth. I., 1883.
- IX. Selenka. Die Sipunculiden-Gattung Phymosoma. Zool. Anz., Bd. xx., 1897, p. 440.
- X. Shipley. A Report on the Gephyrea collected by Mr J. Stanley Gardiner at Rotuma and Funafuti. P. Zool. Soc. London, 1898, p. 468.
- XI. Shipley. On a new species of Phymosoma, etc. Quart. J. Micr. Sci., Vol. xxxii., 1891, p. 111.
- XII. Sluiter. Beiträge zu der Kenntniss Gephyreen aus dem Malayischen Archipel. Natuurk. Tijdschr. Nederl. Ind., Bd. xll., 1881, p. 495.
- XIII. SLUITER. Natuurk. Tijdschr. Nederl. Ind., Bd. XLV.

### DESCRIPTION OF PLATE XVIII.

- Figure 1. Aspidosiphon klunzingeri, Sel. & Bülow, × 2. The introvert is partially everted.
- Figure 2. Aspidosiphon ravus, Sluiter, × 4. The introvert is completely extended and shows the spines near the base and the rows of hooks near the head.
- Figure 3. One of the spines of A. ravus from the base of the introvert, highly magnified.
- Figure 4. A view of a piece of the introvert of Sipunculus australis, Kef., showing the so-called "hooks," and their relation to the rows of glandular papillae. Much magnified.
- Figure 5. A transverse section through three of the cuticular structures called "hooks" of S. australis showing the cuticular caps overlaying the special elevations of the skin.
- Figure 6. Sipunculus billitonensis, Sluiter, × 1.
- Figure 7. A much magnified view of the anus of S. billitonensis.
- Figure 8. Sipunculus cumanensis, Kef., × 1. This specimen shows the violent contractions of the circular muscles which often give specimens of this species a characteristic appearance.



SHIPLEY SIPUNOULCILEA

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## ON THE SOLITARY CORALS, COLLECTED BY DR A. WILLEY.

### BY J. STANLEY GARDINER, M.A.,

Fellow of Gonville and Caius College, Cambridge.

### With Plates XIX, and XX.

The solitary corals, classified and in part described in this communication, are remarkable for the large number of new species. Dr Willey, however, was the first to undertake systematic dredging in the seas of the South-West Pacific. Probably some may ultimately be found to be young forms, but I do not think any of the new species can possibly be stages of growth (or instars) of previously described forms.

The collection in the British Museum, with which the specimens were compared in August, 1897, and subsequently, includes the Challenger specimens and a large number presented by Count de Pourtalès from the West Indies. A comparison with the Porcupine collection would have been of the greatest possible value, but unfortunately these specimens were, I am informed, sold in America. I must here express my great indebtedness to Prof. F. Jeffrey Bell for his very kind assistance and valuable advice.

### FAMILY. TURBINOLIDAE, Milne-Edwards and Haime.

GENUS. Desmophyllum, Ehrenberg.

### 1. Desmophyllum tenuescens, n. sp. (Fig. 1.)

The corallum is inversely conical and light with a smooth, very finely granulated stalk, which may be slightly enlarged at the attached base. The costae are very small and do not extend for more than 1.5 mm. down the outside of the corallum.

The calice<sup>2</sup> is circular or slightly elongate and deep. The septa are thin, very finely granulated on the sides and with entire edges. They are arranged in six systems with three complete cycles. The primaries are 1·1—1·4 mm. exsert and

<sup>1</sup> For explanation of Plates XIX. and XX. see p. 176, et seq.

<sup>&</sup>lt;sup>2</sup> The term calice was first used by Duncan ("Revision of the Families and Genera of the Madreporaria," Jour. Linn. Soc., xvIII. p. 200), for the upper opening of the corallite or corallum. The corallite is an individual member of a colony and the corallum an entire solitary or compound coral.

almost meet in the centre of the calice, nearly obliterating the axial fossa; their upper edges extend nearly horizontally inwards, while their inner edges slope almost perpendicularly down to the axial fossa. The secondaries do not project so far as the primaries, but are thicker and more exsert than the tertiaries, which are very thin and inconspicuous.

Extreme height of the largest specimen, 10 mm. Diameter of the calice of same 5.5 mm. Depth of the calice from the top of the theca to the edges of the septa in the axial fossa 1.5—2 mm.

Loc. Sandal Bay, Lifu; 40 fathoms. Seven specimens.

In spirit specimens of this coral the body-wall can be seen to extend for a short distance down the outside of the theca. As the costae do not generally extend below the body-wall, there would seem to be an epitheca deposited by it completely obliterating them and filling up their intercostal spaces. In one specimen, which has been much overgrown by a sponge, the edge of such an epitheca is distinctly visible, the body-wall having evidently been forced to withdraw itself higher up the corallite.

In the two youngest specimens, which are about 5 mm. in height, the shape of the calice is nearly hexagonal. The three cycles of septa are fully developed, but all are very slightly and equally exsert.

# GENUS. Rhizotrochus, Milne-Edwards and Haime.

## 2. Rhizotrochus levidensis, n. sp. (Fig. 2.)

The corallum is conical and covered by a well developed stout concentrically marked epitheca. There is usually one large radicle with two or three smaller, hollow roots, arising as if from its sides. There are no costae, or costal prominences of the epitheca.

The calice is slightly oval and deep; the wall is formed entirely of the epitheca, no visible theca being present. The septa are not at all exsert, of moderate thickness and entire; their sides are covered with coarse pointed spines. Three distinct eycles in six systems are present. The primaries are much the most conspicuous and meet at the bottom of the very deep, slightly elongated central axial fossa. Slightly below the edge of the epitheca the primaries and secondaries project for some distance nearly horizontally into the calice, ending almost perpendicularly by the axial fossa. Of the primaries two, situated at opposite ends of the axial fossa, are distinctly smaller and slope more gradually inwards than the four at its sides. The tertiaries are very small and narrow, not being more than half as broad as the secondaries.

Extreme height of the largest specimen, 12 mm. Long diameter of the calice of same, 6 mm.; short diameter, 4.6 mm.

Loc. Sandal Bay, Lifu; 40 fathoms. Three specimens.

The two smaller specimens have the calice rather more circular than the largest, whose dimensions are given above. The species is evidently very closely allied to *Rhizotrochus affinis* (Duncan), but separated by its smaller size, more circular form and the presence of only three cycles of septa.

# GENUS. Thecocyathus, Milne-Edwards and Haime.

## 3. Thecocyathus minor, n. sp. (Fig. 3.)

The corallum is cylindrical, straight, of nearly equal diameter throughout, closely covered up to the calicular margin by a dense, glabrous epitheca, which is somewhat transversely marked.

The calice is nearly circular in shape and shallow. The septa are closely arranged with extremely granular sides; they project into the calice for about a quarter of its diameter and are scarcely at all exsert. The arrangement of the septa is hard to distinguish, but each of the six systems has at least six septa, the primaries, secondaries and tertiaries being complete, but the quaternaries only represented by two septa on opposite sides of one of the tertiaries. The primaries are a little thicker and project rather further into the calice than the other cycles which are nearly equal. The centre of the calice is filled up by a large number of very granular, round or elongated papilliform projections which gradually decrease towards the centre; these are the pali and the papillae of the columella. The pali appear to be single in front of the primary and secondary septa, but in front of the latter are generally rather larger, higher and more elongated. Pali also are found opposite the tertiary septa, where quaternaries are present, and usually consist of two or three projecting papillae, which merge into those of the columella.

Height of the single specimen, 7 mm. Diameter of the calice of same, 4 mm.

Loc. Sandal Bay, Lifu; 40 fathoms.

This coral is closely allied to *Thecocyathus cylindraceus* (Pourtalès) from the Florida Reef. It differs, however, in the very irregular arrangement of its pali and its narrow septa.

#### GENUS. Deltocyathus, Milne-Edwards and Haime.

## 4. Deltocyathus ornatus, n. sp. (Fig. 25.)

The corallum is flattened discoidal and free. The inferior surface is almost flat with a slight flattened prominence in the centre almost like the scar of a former attachment. The costae are nearly equally developed; they commence as lines of low, round, blunt granules at the sides of the central prominence, which itself is irregularly covered with similar granules. Towards the margin the costae form a series of rounded ridges and the granulations become sharper and more spiny.

The calice is round, shallow but yet with a large and distinct axial fossa. The septa are very similar in appearance and of nearly equal thickness; their faces are sparsely covered with fine elongated pointed spines. There are six systems and four complete cycles, of which the primaries and secondaries are almost precisely similar, being equally broad, about 1 mm. exsert, and possessing similar elongate paliform lobes. The primaries, however, run rather deeper into the calice and their paliform lobes are rather nearer its centre, higher and more elongated. The tertiaries are not quite so broad as the preceding cycles but extend about as far into the calice as

the secondaries; the exsert portions are about 2.5 mm. in length and pointed, the costae continuing evenly into them but the septa more abruptly broadening where those of other cycles commence; their paliform lobes are more elongated than those of the preceding cycles. The quaternaries are about as exsert as the first two cycles, but do not extend into the calice nearly so far as the other cycles, and fuse with the tertiaries at about the commencement of their paliform lobes. The first three cycles of septa unite with the columella which is large, rather spongy and porous, with an even surface covered by low, small, blunt, subequal papillae.

Extreme diameter of the single specimen, 13.5 mm. Greatest thickness of same 3.4 mm.

Loc. Sandal Bay, Lifu; 40 fathoms.

I do not know any characters by which the primary septa can be satisfactorily differentiated. Six septa are generally broader, rather thicker and more exsert than the rest, and to these the term primary is commonly applied. In the development of Astroides calycularis von Koch<sup>1</sup> has shown that twelve septa are laid down simultaneously, and the study of the structure of the hard and soft parts together has in a variety of genera shown that at least the largest twelve septa are entocoelic. In Fungia, Bourne<sup>2</sup> has pointed out that the first twelve septa to appear run straight to the columella in the adult and are not joined at their sides by other septa. Hence I have here termed those septa (twelve in number), which are the broadest, run deepest into the calice and are not joined by other septa, the primaries and secondaries. Six of these septa are undoubtedly in a large number of genera of Madreporaria larger and more distinct, so that I prefer to apply the term primary to them.

In Deltocyathus italicus, as shown in Pourtalès' plates<sup>3</sup>, the broadest and most exsert septa run singly to the columella. These are the primaries, and the quaternaries can clearly be seen to fuse with the tertiaries. In Deltocyathus magnificus (Moseley<sup>4</sup>) the quinaries fuse with the quaternaries and the latter again with the tertiaries, while the secondaries do not extend quite so far into the calice as the primaries.

### GENUS. Paracyathus, Milne-Edwards and Haime.

## 5. Paracyathus lifuensis, n. sp. (Fig. 5.)

The corallum is low and almost straight, spreading out to form a large, flat, irregular base of attachment. It is also slightly enlarged above forming a somewhat oval calice. The outside of the corallum is marked by subequal, broad ridges with narrow furrows between extending down to the base; these are covered with low granules—often two rows on each ridge—and represent the costae, corresponding in number to the septa.

The septa are large with roughly granular sides and crowded, almost obliterating the interseptal spaces. They form six systems and four complete cycles with a few

<sup>&</sup>lt;sup>1</sup> Mitth. Zool. Stat. Neapel, III. p. 284 (1882).

<sup>&</sup>lt;sup>2</sup> Trans. Roy. Dublin Soc., Vol. v. p. 205 (1893).

<sup>&</sup>lt;sup>3</sup> Cat. Mus. Comp. Zool., Harvard, No. IV. Pl. II. figs. 1 and 5 (1871).

<sup>&</sup>lt;sup>4</sup> Deep Sea Madreporaria, Challenger Reports, p. 148, Pl. xIII. fig. 1.

of the septa of the fifth cycle. The primaries are the largest and everywhere rise about 1 mm. above the tertiaries and quaternaries, which are about 1 mm. exsert and subequal, while the secondaries are intermediate in their characters. The pali are well developed and elongated in the plane of their septa. Usually they are single before the primaries and secondaries, but rather more elongated before the latter, while before the tertiaries they are often bi- or tri-lobed. The columella is depressed about 1 mm. below the pali; it is oval in shape, about 2.5 by 1.4 mm., and consists of a number of small, rounded, granular papillae.

Extreme height of the largest specimen, 10 mm. Long diameter of the calice of same, 9 mm.; short diameter, 7 mm.

Loc. Sandal Bay, Lifu: 40 fathoms. Two specimens.

The two specimens of this species were obtained evidently from the same haul of the dredge, and are almost of the same size. Both are much overgrown at the base by algae, sponges and foraminifera. The epitheca is exceedingly thin and difficult to distinguish. It, however, seems to keep pace with the growth of the incrusting organisms, being deposited closely over the theca and costae as the body-wall is withdrawn.

To the same species I also refer a small specimen 4 mm. high by 2·2 mm. in diameter across the calice. The septa are very similar to those of the type, but quinaries are absent and the quaternaries are only represented by two or three septa. The primaries and secondaries alone have pali, which are single lobed and rather more elongated in front of the secondaries. The columella is represented by a single median papilla.

# 6. Paracyathus parvulus, n. sp. (Fig. 4.)

The corallum tends to be somewhat elongated and is more or less of equal diameter throughout. The outside is marked by very distinct, broad, subequal, granular, ridge-like costae with narrow, deep furrows between. The epitheca is very thin, but closely deposited round the costae and extending up to 3—5 mm. below the calice.

The calice is oval with a deep axial fossa. The septa are broad, granular, slightly exsert and much crowded with small interseptal spaces. Four cycles in six systems are present, of which three are complete, but the fourth is not represented in any of the systems by more than two septa on opposite sides of one of the tertiaries. The primaries are about 0.75 mm. exsert and project for about 1 mm. into the calice. The septa of each cycle are slightly more exsert and broader than those of the cycle next below them, but where quaternaries are developed the tertiaries are enlarged and approximate in size to the secondaries. Rounded pali are present before the primary, secondary and some of the tertiary septa, where quaternaries are present; before the secondaries they are distinctly larger than before the primaries and in front of the tertiaries are sometimes bilobed. The columella is situated rather deeper and ends above with 8—12 very small rounded papillae.

Height of the largest specimen, 16 mm. Long diameter of the calice of same, 4.5 mm.; short diameter, 3 mm.

Loc. Sandal Bay, Lifu; 40 fathoms. Eleven specimens.

This species is extremely variable in its mode of growth, some of the specimens being very short but with their calices almost as large as that of the largest specimen the dimensions of which are given above. In the smaller specimens the calice tends to be more rounded but all its general characters, as given above, are clearly marked. Some of the specimens are attached together, as if growing from a stolon, but there does not seem to be any continuity between them, and the corallites so attached are of approximately the same size.

### FAMILY. ASTRAEIDAE, Dana.

GENUS. Lithophyllia, Milne-Edwards and Haime.

## 7. Lithophyllia vitiensis (Brüggemann).

Scolymia vitiensis, Brüggemann, Ann. Mag. Nat. Hist., Ser. 4, xx. p. 304 (1877).

I have referred one specimen about 1.3 cm. in extreme height by 3 cm. in greatest diameter to this species. The corallum is very irregular in shape, the base having evidently been much worn away by boring organisms, etc. The calice is shallow and considerably filled up by endotheca. The cycles of septa are in parts of the calice rather more distinct from one another than in the type, and the septal teeth are less obtuse.

Loc. Sandal Bay, Lifu; shallow water.

## 8. Lithophyllia palata, n. sp. (Fig. 6)

The corallum is short and very thin with no distinct epitheca. The costae are not pronouncedly marked, but extend down as far as the body-wall and are armed with a number of small, closely set, bluntly pointed teeth.

The septa are very densely granulated at their sides and extend to the columella. There are three complete cycles and six systems; the fourth cycle is nearly complete, and in some of the systems a few spines represent septa of a fifth cycle. The primaries are very thick and distinct, extending inwards at first horizontally with very ragged and broken spiny edges without any large teeth; they then slope steeply with smooth edges towards the columella, before which they generally end each with a large blunt tooth or paliform lobe, rising vertically upwards for 2—2.5 mm. The secondaries are similar in appearance, but towards the columella are very thin with a few pointed teeth and no paliform lobes. The tertiaries and quaternaries are much thinner with numerous subequal pointed teeth. The columella is small and rather open, being formed by the fusion of a large number of small crimpled trabeculae from the septal edges.

Diameter of the calice 1.7-2 cm.

Loc. Sandal Bay, Lifu; shallow water. One specimen.

The single specimen has been attacked and worn away almost to the edge of the calice by incrusting nullipores, etc., so that the costae are scarcely visible. The edge of the calice is rather irregular, the polyp, wherever the nullipore is advancing, endeavouring to grow out above it. The coral, however, can be at once distinguished from all previously described species by the characters of its primary septa. Owing apparently to the irregularity of the calice the paliform lobe is absent from two of the primary septa, and a third primary is distinctly bilobed towards the exterior. There is no sign of any epitheca, the junction of the formerly living extrathecal tissues and dead parts, however, being marked by a distinct thin pellicle, the edge of the advancing nullipore.

### GENUS. Antillia, Duncan.

## 9. Antillia sinuata, n. sp. (Fig. 26.)

The corallum is widely open, trumpet shaped, somewhat bent and twisted. It is attenuate below, being drawn out gradually into a pedicle which in the specimen is bent sharply to one side. The pedicle is slightly compressed in a plane at right angles to its bend, but the calice above is more or less round with the edges rather sinuous.

The epitheca is very thin and transversely lined with the costae in places showing through; it is distant about 1 mm. from the true theca and extends up to about 3 mm. from its edge, above which the septa are 2—3 mm. exsert.

The septa are 102 in number, of which about half fuse with the columella, which closes in the oval axial fossa—8 mm. by 5 mm.—with a mass of twisted, tangled and anastomosing processes. The systems and cycles are not readily distinguished, as about the first 24 septa are almost equal in size; each of these generally possesses a paliform lobe, rising abruptly to a height of 2 mm. above the septal edge, then running horizontally inwards for 3—5 mm. and sloping steeply down to the columella, which is situated about 4 mm below its upper edge. The septa of the fourth and fifth cycles are very irregular in length, and often are fused with the septa of preceding cycles, where the edge of the calice is depressed. The septa of the different cycles are nearly equally exsert and extend down to the epitheca as costae, which project for about 1 mm. from the theca. The edges of the septa are covered by low pointed teeth about 0.5 mm. apart and corresponding to these on the sides of the septa are a number of ridges.

Extreme height of the single specimen, 2.7 cm. Diameter of the calice, 3.5—3.9 cm. Diameter of the pedicle where broken, 3 mm.

Loc. Talili Bay, New Britain; 35 fathoms.

The specimen on which this species is founded has been broken off close to its attached base; in the fractured surface 12 septa and a broad columella are visible. Both exotheca and endotheca are scanty. The epitheca is attached to the corallum chiefly by means of the costal edges, and near the base has been much worn away by algal and worm growths.

The species is in its characters to some extent intermediate between Antillia explanata (Pourtalès) from Barbadoes and Antillia constricta (Brüggemann) from Borneo.

### GENUS. Tridacophyllia, Blainville.

### 10. Tridacophyllia primordialis, n. sp. (Fig. 7.)

The corallum is somewhat conical below, and attached by a stout pedicle with a slightly spreading base. The margin of the calice grows out into four thick, pointed branches. Of these, two arise opposite to one another and grow almost vertically upwards, the axial fossa between being generally somewhat elongated in the plane at right angles. Between these, in the latter plane, two more branches grow almost horizontally outwards, of which one is from the first usually much longer than the other; neither, however, attains the same length as the vertical branches. The outside of the corallum is marked by longitudinal rows of fine granules, which can be seen to be continuous with the costae and slightly exsert septa above.

The septa are thick with very finely granular sides and almost smooth edges. Their arrangement into cycles and systems is difficult to distinguish. Twelve extend to the axial fossa, of which one reaches to the top of each branch and two to its sides. Between these, three septa are usually intercalated so that four cycles would seem to be present. The interseptal loculi are shallow, being closed in below by endotheca. The axial fossa is elongated, rather narrow and open without any sign of a columella.

Extreme height of the largest specimen, 15 mm. Length of its vertical branches, 5 mm. and 5.5 mm. Length of the horizontal branches, 3.5 mm. and 1 mm.

Loc. Sandal Bay, Lifu; 40 fathoms. Five specimens.

A careful comparison of the specimens of this species with those of *Tridacophyllia cervicornis* (Moseley) in the British Museum has convinced me that this species is not a young form of it. The regular method of branching, the thickness of the branches, the considerable development of endotheca and the smooth edges of the septa in *Tridacophyllia primordialis* serve at once to distinguish between the two species.

In the youngest form, which is about 4 mm. high, the vertical branches are just beginning to grow out. Six septa run to the axial fossa; two of these run to the sides of each of the vertical branches, while the remaining two form ultimately the central septa of the two horizontal branches.

### FAMILY. FUNGIDAE, Milne-Edwards and Haime.

Genus. Fungia, Milne-Edwards and Haime.

### 11. Fungia ehrenbergii, Leuckart.

Herpetolithus ehrenbergii, Leuckart, De Zooph. Corall. et gen. Fungia, p. 52, tab. II. (1841).

Fungia ehrenbergii, Dana, Zooph., p. 303, Pl. XIX., fig. 2 (1846).

There is one free anthocyathus, 10·2 cm. long by 4·4 cm. in breadth, which is referable to this well marked species. In addition there are four fixed specimens, which seem not improbably to belong to the same species.

Loc. Blanche Bay, New Britain; shore reefs.

GENUS. Cycloseris, Milne-Edwards and Haime.

12. Cycloseris hexagonalis (Milne-Edwards and Haime).

Fungia hexagonalis, Milne-Edwards and Haime, Ann. des Sc. Nat., Ser. 3, t. IX., Pl. VI., fig. 2 (1848).

I have referred one adult anthocyathus without any scar of attachment and fifteen young specimens to this species. The young forms do not show the hexagonal characters of Milne-Edwards' specimens. A full description, however, will be given later.

Loc. Blanche Bay, New Britain; shore reefs.

FAMILY. EUPSAMMIDAE, Milne-Edwards and Haime.

GENUS. Balanophyllia, Searles Wood.

13. Balanophyllia profundicella, n. sp. (Fig. 9.)

The corallum is almost straight, cylindrical, attached by a spreading base. The wall is devoid of epitheca, the living tissues covering about the upper third. The costae correspond to the septa, and are broad, subequal and little projecting with narrow intercostal spaces at the bottom of which the theca is but slightly perforated.

The calice is slightly oval in shape with a very deep, central, axial fossa. The septa are rather thin; their sides appear almost smooth, being covered with very minute granules, and their edges are entire. They are arranged in six systems and four cycles, all of which are complete. The primaries are prominently exsert, the quaternaries on either side of them and the secondaries projecting to about half their height. The primaries and secondaries are rounded at their summits and end almost perpendicularly by the axial fossa, the former extending furthest into the calice. The quaternaries fuse deep down in the corallum over the tertiaries and again over the secondaries, but the arrangement is not distinct and these septa appear often to be fused with them. The axial fossa is closed in below by the fusion of all the quaternaries very deep down in the calice.

Greatest height of the single specimen. 11 mm. Long diameter of the same, 5 mm.; short diameter, 4·1 mm.

Loc. Sandal Bay, Lifu; 40 fathoms.

W.

This coral comes near *Balanophyllia parvula* (Moseley) from the Philippine Islands. It differs, however, in its more elongate form, deeper axial fossa and in the quaternaries on each side of the primaries being less enlarged.

### Genus. Thecopsammia, Pourtalès.

14. Thecopsammia regularis, n. sp. (Fig. 8.)

The corallum is straight, almost the same diameter from base to calice, with a thin epitheca, extending over about three-quarters of its height and somewhat transversely marked with a well-defined upper edge. Above the epitheca costae are absent,

J. S. Gardiner, "On the postembryonic development of Cycloseris." This volume, p. 171.

but the perforations of the theca are rather large and arranged in lines between the septa so that the edges of the latter are quite distinct, although nowhere projecting outside the thecal structures.

The calice is slightly oval in outline with a very deep elongated axial fossa; its edge has rather a ragged appearance from the slightly exsert septa. The septa are thick with narrow interseptal loculi; they are slightly perforated, and have their sides covered with small granular spines, which may form striae; their edges are bluntly lobed. They are arranged in six systems and four cycles, which gradually decrease in size. The quaternaries are incomplete, in some systems only two, viz. those on each side of one of the tertiaries, being present. The primaries and secondaries and the tertiaries also, if quaternaries are present, fuse with the columella, which is small, rather elongate in shape and formed of twisted lamellae, which may have one or two papilliform projections.

Extreme height of the largest specimen, 9.5 mm. Long diameter of the same, 5.5 mm.; short diameter, 4.3 mm.

Loc. Sandal Bay, Lifu; 40 fathoms. Two specimens.

This species differs from all previously described forms in the marked distinctness of its cycles of septa and in the secondaries and tertiaries being always larger than the quaternaries.

Zoological Laboratory, Cambridge. Aug. 9, 1898.

# ON THE POSTEMBRYONIC DEVELOPMENT OF CYCLOSERIS.

## By J. STANLEY GARDINER, M.A.

With Plate XIX. (Figs. 10-14) and Plate XX. (Figs. 15-24).

When the alternation of generations in Fungia was first described by Stutchbury<sup>1</sup>, the species of Cycloseris, then known, were placed under that genus or the genus Cyclolites. Milne-Edwards and Haime, in 1849, separated the genus Cycloseris<sup>2</sup>, and, in 1851, carefully considered and described its species<sup>3</sup>. In the work last referred to, the genus is described as follows:—"Polypier simple, libre et sans traces d'adhérence, etc." In 1848, the same authors had previously described with a plate the septal arrangements in the different postembryonic stages of Fungia patellaris and Fungia (now Cycloseris) hexagonalis<sup>4</sup>, apparently believing that the development proceeded by similar stages in both species. Among the specific characters of the latter species, however, there is the statement "on ne distingue aucune trace d'adhérence même dans les trèsjeunes individus<sup>5</sup>."

In 1879, Tenison-Woods described a young detached specimen of Cycloseris sinensis<sup>6</sup>, and further stated that a central disk on the under surface "is found on the lower part of every Australian specimen." Quelch considered that the form referred by Tenison-Woods to Cycloseris sinensis was more closely allied to Cycloseris discus and Cycloseris freycineti<sup>7</sup>; he neglected, nevertheless, to mention the fact that some of the Challenger specimens of that species have a very distinct scar on the aboral surface. Bassett-Smith, however, found among his corals from the Tizard and Macclesfield Banks young fixed forms of Cycloseris tenuis and Cycloseris sinensis<sup>8</sup>.

Considering that similar stages to those, so carefully and accurately described for

¹ "An Account of the Mode of Growth of Young Corals of the Genus Fungia," Trans. Linn. Soc., 1830, p. 494.

<sup>&</sup>lt;sup>2</sup> Compt. rend. de l'Acad. des Sci., t. xxix, p. 72.

<sup>&</sup>lt;sup>3</sup> Ann. des Sci. Nat., Ser. 3, t. xv, p. 111.

<sup>4</sup> Ann. des Sci. Nat., Ser. 3, t. 1x, p. 37, Pl. vi.

<sup>&</sup>lt;sup>5</sup> Ann. des Sci. Nat., Ser. 3, t. xv, p. 111, and Cor. 111, p. 51.

<sup>&</sup>lt;sup>6</sup> Proc. Linn. Soc. of N. S. W., vol. III, p. 20.

<sup>7</sup> Reef-Corals, Challenger Reports, p. 122.

<sup>&</sup>lt;sup>8</sup> Ann. and Mag. Nat. Hist., Ser. 6, vol. vi, p. 446 (1890).

Fungia by Bourne<sup>1</sup>, would ultimately prove to be of very wide distribution among the discoid forms of the Madreporaria, I carefully collected in Rotuma and Fiji all the fixed solitary reef-corals I found, upwards of fifty in number<sup>2</sup>. All these were young Fungia with the exception of three or four, which seemed to me to be referable to the genus Cycloseris. On Dr Willey's return he kindly handed over to me two adult and twenty-four young specimens, which he had collected at low tide in rock pools at the base of the cliffs in Blanche Bay, New Britain. One of the adults I have referred to Cycloseris hexagonalis, while fifteen of the young specimens form an almost complete series to it. Two oval anthocyathi with very distinct scars on their aboral surfaces, evidently but recently detached from their anthocauli, are referable to another and probably new species of Cycloseris, which I do not propose to describe as it is not clear how far they have as yet attained their adult characters.

Cycloseris differs from Fungia as described by Duncan<sup>3</sup> mainly in the fact that the theca in the former is imperforate. The septa of the species of the former, that I have examined, as compared with Fungia, are not at all, or not nearly so markedly ridged. The spines on their sides are arranged perfectly regularly, a line along each ridge, or in lines, which diverge in a similar manner to the ridges of Fungia<sup>4</sup>, and are not scattered irregularly over their surfaces. The theca further extends to a definite distance from the ends of the septa, and is not irregularly cut into between them as in Fungia. The synapticula are similar to those of Fungia, but do not extend so high above the theca, nor so far outwards between the septa. They do not in fact give nearly the same support to the corallum as those of Fungia.

The earliest fixed stage of growth or instar, that I have examined, is a young trophozooid 5, 0.4 mm. in diameter by about the same in height (Fig. 10). It is attached to the aboral surface of a dead anthocyathus, which also has growing on it an anthocaulus. The base of the latter and the dead anthocyathus are both much overgrown by incrusting Polyzoa, Foraminifera, Sponges and Worm-tubes. The young trophozooid

- <sup>1</sup> "On the Postembryonic Development of Fungia," Sci. Trans. Roy. Dublin Soc., vol. v. p. 205 et seq. (1893). Vide also "On the Anatomy of the Madreporarian Coral Fungia," Q. J. M. S., xxvII, p. 359, by the same author.
- <sup>2</sup> A careful examination of these specimens has shown me that they very fully confirm Bourne's account so far as it applies to the gross structure of the skeletal parts in the different stages. It seems to me to be probable, though, that stalked individuals may be budded off from the free anthocyathus, where conditions are unfavourable for its continued growth, owing to incrusting organisms, sand, etc. These afterwards may themselves become anthocauli, detaching anthocyathi.
  - <sup>3</sup> Jour. Linn. Soc. Zool., vol. xviii, pp. 141 and 149.
- <sup>4</sup> Comp. "Microscopic and Systematic Study of Madreporarian Types of Corals." By Maria Ogilvie. Phil. Trans. Roy. Soc., vol. clxxxviii, p. 83 et seq. fig. 37.
- $^5$  I have throughout used the terms proposed by Bourne for the different instars of Fungia (loc. cit., p. 206);—
  - Trophozooid. The individual Caryophyllia-like form developed directly from the ovum.
  - Anthoblasts. Buds from the trophozooid.
  - Anthocyathus. The discoid Fungia form, whether free or attached, developed from a trophozooid, or an anthoblast.
  - Anthocaulus. The pedicle, which carries the anthocyathus, and after the detachment of the latter usually gives rise by re-growth to a new anthocyathus.

The term "instar" was advocated by Sharp (Camb. Nat. Hist., vol. v, p. 155) for the successive stadia of insects. It seems to me that the term may be very usefully applied here to imply simply a stage of growth.

is straight and incrusted by a Polyzoon right up to the edge of the calice, which is accordingly bent slightly inwards. There are seven septa at nearly equal distances from one another round the calice, but six are subequal, broad, thick and covered with rough spines while the seventh is comparatively narrow and smooth; the former are termed throughout the primaries. In the centre of the calice is a single prominent, rough papilla—the columella.

The next two instars are also attached to the aboral surface of the same dead anthocyathus. The second is about 0.7 mm. in diameter by 0.5 mm. high, and was apparently covered up to the edge of the calice by an incrusting sponge, which grew to some extent over its opening. The septa are difficult to distinguish, but ten or eleven seem to be present, some of which are very narrow and rudimentary; the columella is deeper and less prominent than in the preceding instar. Attached close to the base of this form is another trophozooid of almost the same size, which has been completely killed by the same sponge; it appears to have ten septa, subequal in size.

The third instar (Fig. 11) is straight, about 1.2 mm. in diameter by 0.7 mm. in height. Fourteen septa are present, which cannot however be distinguished into cycles. Two are extremely thin and rudimentary, while four others do not appear to fuse with the rest in the centre of the calice; the remainder vary in thickness and are slightly exsert with rough granular spines. The axial fossa is deep, about 0.4 mm. broad and closed in below by the fused septal trabeculae from which project three large, rough papillae, one of which lies almost centrally, and is, I believe, the true columella. The wall is covered on the outside by an incrusting alga; it appears to be in some places double and to consist of a fused theca and epitheca.

The above forms are, I believe, true trophozooids, directly developed from the ovum. In many of the succeeding instars it is impossible to see whether the young form has been developed from a trophozooid, an anthoblast (if such exist), or by the re-growth of an anthocaulus. The development of the skeletal parts appears to follow along the same lines so that I shall briefly describe them, mentioning to

which category each form seems to belong.

The next instar (Fig. 12) has 28 septa. It is the re-growth of a nearly straight anthocaulus from which three anthocyathi—the lower two represented by rings—appear to have separated at the heights of 4, 6.5 and 8 mm. above its attached base. The anthocaulus where the last anthocyathus separated is about 3.5 mm. in diameter while the young anthocyathus is still straight, about 1 mm. high by 2 mm. in diameter. The six primary septa can be clearly distinguished, being thicker, more spinulose and markedly broader than the rest. The remainder vary considerably, one of the secondaries being almost as thick and exsert as the primaries, but clearly joined at its sides by two of the tertiaries. The axial fossa is large and closed in below by a trabecular columella, with which most of the septa appear connected.

The commencement of the horizontal growth is clearly seen in another specimen (Fig. 13), formed by the re-growth of an anthocaulus, from which one anthocyathus has separated. The calice is about 7 mm. in diameter while the stem is 3.5 mm. Four cycles of septa are complete and there are also 8 septa of the fifth cycle. The primaries are quite distinct while the quaternaries are fused to the tertiaries, which are

themselves fused to the secondaries. A few synapticula—formed apparently by the fusion of spines on the sides of the septa—are found close to the axial fossa, which begins to attain its adult appearance, closed in below by a spongy, trabecular columella with small, blunt, papilliform projections.

Another anthocyathus (Fig. 23), about 13 mm. across the calice, on an anthocaulus with three rings, attached to the same dead Cycloseris as the first three instars, shows the still further horizontal growth. Four cycles of septa are complete and the fifth nearly so; all are slightly exsert.

The theca is imperforate in all the specimens; it is formed in the same way as in Fungia by the fusion of the swollen-out sides of the septa. Fresh centres of calcification appear to be intercalated as the circumference of the calice becomes greater and the distance between the septal ends is increased; these give rise to the fresh cycles of septa. Some of the septa in the last instar are over 1 mm. exsert while in the adult none project for more than 3 mm. beyond the theca. The synapticula vary extremely, but in no specimens extend within 2 mm. of the edge of the theca.

The remaining fixed specimens are (i) an anthoblast (or trophozooid), 13 mm. in diameter, but very irregular, with 4 complete cycles of septa and the fifth cycle nearly complete (Fig. 24); (ii) an anthocyathus on an anthocaulus, attached to a bud from a dead free form, 17 mm. in diameter, with 5 cycles and a few septa of the sixth (Fig. 22); (iii) an anthocyathus on an anthocaulus with two rings, 26 mm. in diameter, with 6 cycles; (iv) an anthocyathus on a trophozooid, 31 mm. in diameter, with 6 cycles and a few septa of the seventh (Fig. 21); (v) a very irregular anthocyathus on an anthocaulus, 37 mm. in greatest diameter, with 6 cycles and in places the seventh complete also (Fig. 20).

The smallest of these forms (Fig. 24) is 19 mm. high with a relatively deep calice, and attached by the side of its stalk. From a comparison with the instars of Fungia, which I collected myself, I am inclined to believe that it is rather an anthoblast than a trophozooid. In all the rest at the top of the stalk immediately under the horizontal anthocyathus there is a distinct pitted ring (Fig. 21 b), where the break would ultimately have taken place. Above this the corallum is white and translucent while below it is dark and opaque, showing that it is to some extent changed. The part between this and the top ring is in no case overgrown by organisms, and it seems to be probable that the body-wall of the polyp formerly covered it. The detachment of the anthocyathus would seem, indeed, to be effected in precisely the same way as Bourne has described for Fungia. The costae vary, in some being almost smooth ridges and in others having the adult characters.

The smallest free anthocyathus is slightly oval in shape, 20 mm. by 17 mm. in diameter (Fig. 19). On the aboral surface the scar is well marked, but the opening from the exterior into the coelenteron has been closed by corallum, owing apparently to thickenings of the sides of the septa. A slightly larger but irregular form, 23 mm. in greatest diameter, has the opening still complete (Fig. 18). The broken edges of the septa have an extremely opaque, white colour; and above them the septa and trabecula of the columella appear to have been thickening so as completely to close in the coelenteron. The scar is somewhat oval, 6.5 by 5 mm. in diameter, and in it the

septa of the first four cycles can be distinguished (Fig. 14). The aboral surface round the scar has been much overgrown by Polyzoa, and in the smaller free form the corallum is very dense round it so that the costae cannot be traced into its septa. Another specimen triangular in shape, 25 mm. in diameter, has the scar very distinct with the costae quite continuous into its septa (Fig. 17); it has also been overgrown by organisms except for a few mm. round the edge. A larger anthocyathus 5.3 mm. in diameter has the scar still distinct with the septa quite visible (Fig. 16); otherwise its characters are those of the adult. The oral and aboral surfaces of the latter are represented in Figs. 15 a and 15 b. The scar has been completely obliterated and covered over by corallum, its position being merely indicated by a slight opacity.

The striking resemblances between the developments of Cycloseris and Fungia cause a doubt as to the distinctness of these two genera. The differences, mentioned above, between them, are undoubtedly worthy of generic rank, but the two forms are evidently extremely closely allied. The primary septa in Cycloseris are very definitely six in number, the secondaries not reaching quite so far into the calice and having the tertiaries fused to them. In the youngest instar that I examined there are six thick, subequal septa, and in the youngest Fungia found by Bourne "twelve septa are present of which six are distinctly larger than the others." In nearly all the solitary imperforate Madreporaria, which are the more ancient in respect to time, six septa are very strongly marked, and must be regarded as the primaries. In many forms too only six septa are present, and these so far as is known are always entocoelic. The formation of twelve septa simultaneously in Astroides calycularis, of which six later get larger, I can only regard as a condensation of the stages of its development1. It seems to me that primitively there are six entocoelic septa, a number that corresponds with the twelve mesenteries found in the embryos of many of the Actiniaria, and in the embryo also of Euphyllia 2 at the same stage apparently as the fixing larva of Astroides calycularis.

In conclusion, I wish to thank Mr Adam Sedgwick, Dr Willey and others for their kindly interest and advice.

Zoological Laboratory, Cambridge, August 21, 1898.

Vide "Développement des Coralliaires." H. de Lacaze Duthiers. Arch. de Zool. Exper. et Gen., I. and
 II. (1872 and 1873). Also G. von Koch, Mitt. aus der Stat. Zool. Neapel, III. 1882, p. 284.
 The Newly-Hatched Larva of Euphyllia." A. C. Haddon. Sci. Proc. Roy. Dublin Soc., p. 117, 1890.

#### EXPLANATION OF PLATES XIX. AND XX.

#### PLATE XIX.

(The small numerals at the sides of several of the figures refer to the cycles of septa.)

### Fig. 1. Desmophyllum tenuescens, n. sp.

- (a) Profile view of the corallum ( $\times 3\frac{1}{4}$ ). The stalk is covered with small, low granules, the costae only extending for about 1.5 mm. below the edge of the theca.
- (b) The calice from above (× 4). Primary, secondary and tertiary cycles of septa are present, the two former nearly meeting in the centre of the oval axial fossa.

### Fig. 2. Rhizotrochus levidensis, n. sp.

- (a) Profile view of the corallum ( $\times$  3), showing the large radicle and two small rootlets. The epitheca is concentrically marked below, but covered above by incrusting organisms.
- (b) The calice from above  $(\times 3\frac{1}{2})$ . The axial fossa is large and deep but closed in below by the fusion of the primary septa, of which the two, situated at its ends, arise rather deeper and are less projecting.

#### Fig. 3. Thecocyathus minor, n. sp.

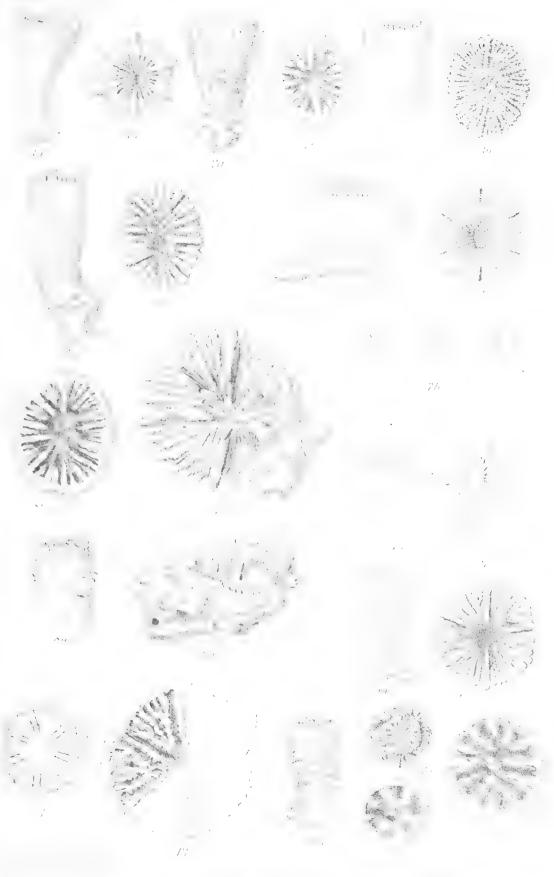
- (a) Profile view of the corallum  $(\times 4\frac{1}{2})$ . The epitheca extends almost to the margin of the calice and is transversely marked. Near the attached base it has been eaten away by boring organisms and the costae are exposed.
- (b) The calice from above (×7). The primary, secondary and tertiary septa are complete; the quaternary are generally represented by two septa in each system on opposite sides of one of the tertiaries. The pali of the primary septa are smaller than those of the secondaries, while in front of the tertiaries bilobed pali are found where quaternaries are present. The columella ends above in blunt papillae with difficulty distinguishable from the pali. The quaternary septa are not quite so completely developed as the figure portrays.

### Fig. 4. Paracyathus parvulus, n. sp.

- (a) Profile view of the corallum  $(\times 3)$ . The lower part is incrusted by a nullipore, while a Polyzoon has grown up on one side to within a few mm. of the edge of the calice.
- (b) The calice from above  $(\times 6)$ . Three cycles of septa are complete, and in some of the systems quaternaries are found on opposite sides of one of the tertiaries.

#### Fig. 5. Paracyathus lifuensis, n. sp.

- (a) Profile view of the corallum (× 3). The costae are subequal broad ridges extending to the somewhat enlarged base of attachment which is overgrown by nullipores, worm-tubes, etc. No epitheca can be distinguished.
- (b) The calice from above ( $\times$  3). The pali in front of the tertiary septa are often bi- or tri-lobed, and are much larger than those of the primaries and secondaries, which themselves project further into the calice.



### Fig. 6. Lithophyllia palata, n. sp.

- (a) Profile view of the corallum (× 2). The base and sides of the corallum are much overgrown by an incrusting nullipore, some of the branches of which can be seen to the left. In consequence of this the costae are, on the side shown in the figure, inconspicuous. The primary septa are much larger and more exsert than the others, and in front of four of them straight, paliform lobes can be seen.
- (b) The calice from above (×2). Owing probably to the irregularity of the calice, paliform lobes are only found in front of four of the primary septa instead of the whole six as normal. The first three cycles of septa are complete; the quaternaries are nearly so, and in some of the systems septa of a quinary cycle are found.

## Fig. 7. Tridacophyllia primordialis, n. sp.

- (a) Profile view of the youngest corallum (× 2). The two vertical branches are commencing to grow out, and the costae are in this stage especially well marked. At the base a small worm-tube is attached.
- (b) Profile view of another young corallum ( $\times$  2), in which one of the vertical branches is much longer than the other.
- (c, d and e). Profile views of older coralla  $(c \text{ and } d \times 2, e \times 3)$ , showing variations in the mode of growth. Four cycles of septa are present, of which the six primaries extend one to the ends of each of the horizontal, and two to the sides of each of the vertical branches. The corallum (e) is partially covered at its base by an incrusting Polyzoon.

### Fig. 8. The copsammia regularis, n. sp.

- (a) Profile view of the corallum ( $\times$  3), showing the high extension of the epitheca, above which is seen the theca with its perforations in lines between the septa. No costae are present.
- (b) The calice from above  $(\times 6)$ . The first two cycles of septa are complete and fuse with the columella, which is formed of twisted lamellae. The tertiaries are likewise complete and there are at least two quaternaries in each system on opposite sides of one of the tertiaries. (The bluntly lobed character of the septal edges is not clearly shown.)

### Fig. 9. Balanophyllia profundicella, n. sp.

- (a) Profile view of the corallum  $(\times 2\frac{1}{2})$ . The costae are subequal and well marked, the theca being little perforated between. The lower part of the corallum is much overgrown by calcareous organisms and there is no epitheca.
- (b) The same from above  $(\times 5)$ . Three cycles of septa are complete and the fourth nearly so. The quaternaries fuse over the tertiaries and again over the secondaries, joining then deep down in the calice with the primaries so as to close the axial fossa below.
- Figs. 10—24. Various stages in the postembryonic development of *Cycloseris hexagonalis*, Milne-Edwards and Haime.
- Fig. 10. Oral view of a young trophozooid (× 25) with seven septa, of which six are much broader and fuse below with the columella. The edge of the corallum appears smooth and slightly bent inwards owing to incrusting organisms growing over its sides.

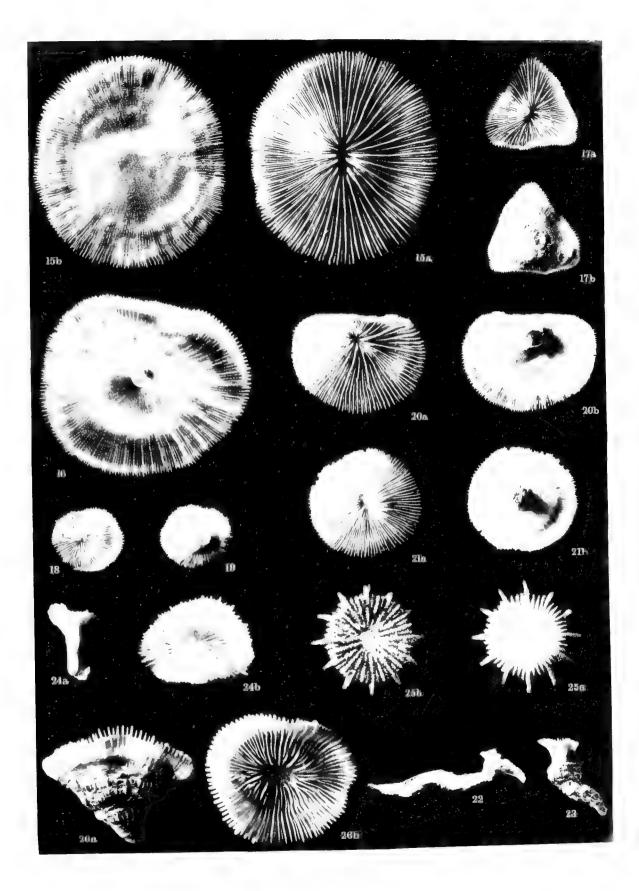
- Fig. 11. Oral view of a slightly older trophozooid (x 25) with fourteen septa, of which twelve—the primaries and secondaries—are conspicuously the larger. The sides of the corallum are overgrown by an incrusting sponge, which extends up to the edge of the calice, and gives it a smooth, regular appearance.
  - Fig. 12. Commencing regrowth of an anthocaulus to form a new anthocyathus.
- (a) Profile view  $(\times 3\frac{1}{2})$ , showing two rings of detachment of previous anthocyathi. The top is flat owing to the recent separation of a third anthocyathus, and in its centre can be seen a new anthocyathus being formed by its regrowth.
- (b) Oral view (x 5). After an old anthocyathus has become detached, a new anthocyathus commences to grow out from the centre of the scar on the anthocaulus, the outer part dying. Subsequently the stalk of the new anthocyathus broadens and attains about the same breadth as the anthocaulus below it. Many of the septa of the bud can be seen to be in the same vertical plane as those broken off, where the previous anthocyathus became detached, the septa of the bud being continuous with those left in the anthocaulus.
- Fig. 13. Oral view of an anthocyathus formed by the regrowth of an anthocaulus ( $\times$  6), showing the commencement of the horizontal growth. Four cycles of septa are complete: of these the quaternaries fuse with the tertiaries and the latter with the secondaries, while the primaries run straight to the axial fossa, which is closed in below by the relatively large, papilliform columella.
- Fig. 14. Scar on the aboral surface of the recently freed anthocyathus shown in Fig. 18 ( $\times$   $3\frac{1}{2}$ ). The corallum is still open between the oral and the aboral surfaces, but the septa, of which four cycles can be seen in the scar, have begun to thicken at their sides. Their edges are extremely white and opaque, the corallum having evidently undergone a change which probably brought about the separation of the anthocyathus.

### PLATE XX.

(The figures on this plate, unless otherwise precisely stated, are all of the natural size.)

Figures 15—24 relate to Cycloseris hexagonalis,

- Fig. 15. An adult anthocyathus.
- (a) Oral view. The six primary septa except at the ends of the axial fossa can be seen to project slightly further into the calice than the secondaries. The septa of higher cycles can be seen in places very distinctly fusing with those of the cycles below them.
- (b) Aboral view. The corallum has a well marked imperforate theca, beyond which the septa are nearly equally exsert. In the centre is a slightly opaque area covered with low spines where the anthocyathus originally separated from its stem.
- Fig. 16. Aboral view of the next oldest anthocyathus, in which the scar is still very conspicuous. The costae are well marked rows of blunt spines, extending almost to the scar.





- Fig. 17. An aberrantly shaped free anthocyathus with six cycles of septa.
  - (a) Oral view.
- (b) Aboral view showing the scar still very distinct. The whole surface has been much overgrown and killed except near the edges by incrusting organisms. Some of the costae, however, can be directly traced into the septa of the scar.
- Fig. 18. Oral view of the young free anthocyathus, the scar of which is represented in Fig. 14. Five cycles of septa are complete.
- Fig. 19. Aboral view of the smallest free anthocyathus. The corallum is nearly closed in below, but the edges of the septa in the scar are still very ragged and distinct.
  - Fig. 20. A large irregular, attached anthocyathus.
- $(\sigma)$  Oral view. Six cycles of septa are complete and on the broad side the seventh cycle also.
- (b) Aboral view. In the centre is the stem, to which the anthocyathus is attached. It is an anthocaulus, from which one anthocyathus has already separated, the ring left by which can be seen in places.
  - Fig. 21. An anthocyathus almost ready apparently to detach itself from its stalk.
    - (a) Oral view showing six complete cycles of septa.
- (b) Aboral view. In the centre is the stalk, round which immediately under the horizontal outgrowth can be seen a distinct pitted ring, where the anthocyathus will subsequently be detached.
- Fig. 22. Profile view of a young anthocyathus, attached to an anthocaulus, which is itself fixed on a dead free anthocyathus, from which it was probably in the first place budded. There is one ring of detachment of a former anthocyathus.
- Fig. 23. Profile view of a still younger anthocyathus on an anthocaulus with three rings. Even at this size a trace of the pitted ring, where the anthocyathus will subsequently be detached, is visible. The anthocaulus is attached to a fragment of a dead free anthocyathus, to the under surface of which the three youngest trophozooids, two of which are represented in Figs. 10 and 11, are attached.
  - Fig. 24. A young anthoblast (trophozooid?) with four cycles of septa complete.
    - (a) Profile view  $(\times 1)$ .
    - (b) Oral view ( $\times 2\frac{1}{4}$ ).
  - Fig. 25. Deltocyathus ornatus, n. sp.
- (a) Aboral view ( $\times 2\frac{1}{4}$ ). The costae commence as rows of low granules, gradually passing from a slight prominence in the centre into broad rounded ridges towards the exterior. The primary, secondary and quaternary septa are equally exsert, while the tertiaries—twelve—project considerably further.
- (b) Oral view ( $\times$   $2\frac{1}{4}$ ). The primary and secondary septa closely resemble one another, but can be seen in most of the systems to run much deeper into the corallum and to have less elongated paliform lobes than the tertiary septa, which are much more exsert. In places the quaternary septa can be seen bending in towards the tertiaries with

which they fuse deeper in the corallum. (The exsert portions of two of the tertiary septa at the top right-hand corner of the figures are broken.)

# Fig. 26. Antillia sinuata, n. sp.

- (a) Profile view of the corallum. The epitheca is very thin and extends up to about 3.5 mm, from the edge of the calice. Below it has been worn away by various organisms and the costae are exposed. The pedicle of the corallum is broken.
- (b) The calice from above. There are 102 septa, the lower cycles of which are not readily differentiated. The columella is a mass of tangled and anastomosing processes arising from about half of the septa.

ON A COLLECTION OF EARTHWORMS FROM NEW BRITAIN, THE SOLOMON ISLANDS, THE NEW HEBRIDES, AND THE LOYALTY ISLANDS.

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Prosector and Assistant Secretary of the Zoological Society.

With Plate XXI.

THE following pages relate to the Collection of Earthworms formed by Dr Willey among the islands mentioned in the title. A very considerable number of these worms were in an excellent state of preservation; others on the contrary were softened. In the case of the latter I have not thought it advisable in every case to publish a description. I have taken this course on account of the fact that I could not be quite certain as to their identity or non-identity with other species. It appears to me that little is gained by publishing an account of a species which cannot, from the nature of the case, be sufficiently full to permit of a confident statement as to its specific characters, unless indeed new details of anatomical importance should turn up during the examination. This applies also to immature examples, of which Dr Willey's collection contained a good number. Such incomplete descriptions would only serve to exercise the ingenuity of workers coming after me, who might consider it to be their duty to identify species with those briefly described by myself; no advantage to science would be gained by taking this step. I shall therefore deal in this memoir only with those species which I can, I believe, fully identify as new forms or as species already known.

The area where Dr Willey collected the species to be described here is a large one, and has not been much investigated from the point of view of its earthworm inhabitants. It may be convenient before adding my own contributions to the knowledge of the Earthworms of the Polynesian region (of Lydekker) and of the islands adjacent to New Guinea, to refer briefly to what has already been done.

I shall consider only New Guinea and the islands which lie to the west of Long. 150, below the equator and to the north of New Zealand.

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The first accounts of earthworms from this tract of the earth's surface are contained in the memoir of Kinberg entitled "Annulata nova" which was based upon the collection made during the voyage of the Swedish vessel "Eugenia1." are perfectly unrecognisable and need not detain us; they are Lumbricus tahitana (from Tahiti), which is possibly a Cryptodrilid: Pheretima montana from the same island, which is clearly a Perichaetid, and probably a Megascolex, judging from the length of the clitellum. Grube described in the "Voyage of the Novara" Perichaeta taitensis from Tahiti, and P. subquadrangula from Viti. The former of these species Rosa<sup>3</sup> divided into two to which he gave the names of P. grubei, and P. novarae. The latter species of Grube may be my P. vitiensis. From the island of Upolu in the Samoa group I described some years since P. upoluensis. From New Guinea I described P. forbesi<sup>8</sup>, and subsequently Michaelsen<sup>7</sup> founded the species P. neoquinensis. More recently still Rosa<sup>8</sup> has described a variety of Michaelsen's species as well as P. loriae and P. papua from that same island. Dr Benham<sup>9</sup> examined some of Dr Willey's collection and founded upon the material sent to him from New Britain the species P. novae-britannicae, P. sedgwickii and P. arturi.

The very widely distributed P. indica was found by myself in a gathering of earthworms from New Caledonia<sup>10</sup>, and from that same island Perrier described Acanthodrilus  $ungulatus^{11}$  (which is not perhaps separable from my A. layardi). I have also recorded the ubiquitous Eudrilus  $eugeniae^{12}$  from New Caledonia. Dichogaster  $damonis^{13}$  is a Fijian species. The genus Benhamia is represented in New Guinea by B.  $malarmata^{14}$ .

In the present communication I describe as new forms the following species:—

Perichaeta pacifica, New Britain.

Perichaeta solomonis, from Narowol and New Georgia (Rubiana) of the Solomon Archipelago.

Perichaeta esafatae, Esafate, New Hebrides.

I also am able to extend the range of *Perichaeta upoluensis* to the New Hebrides, of *Perichaeta malamaniensis* to the New Hebrides and Loyalty Islands, and of *Perichaeta loriae* to the Solomon Islands.

In addition to these species of *Perichaeta* the collection contained examples of *Benhamia* from New Britain and from Lifu which I did not further identify.

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<sup>1</sup> In Övers, k. vetensk. Ak. Handl., 1866, p. 97 et seq.
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<sup>&</sup>lt;sup>2</sup> Anneliden in Novara Expedition.

<sup>&</sup>lt;sup>3</sup> Ann. k. Hofmus. Wien, vr. 1891, pp. 35-37.

<sup>&</sup>lt;sup>4</sup> Ann. and Mag. Nat. Hist., 1892, p. 131.

<sup>&</sup>lt;sup>5</sup> Proc. Roy. Soc. Edinb., xiv. p. 174.

<sup>&</sup>lt;sup>6</sup> P. Z. S., 1890, p. 65.

<sup>&</sup>lt;sup>7</sup> Arch. f. Naturg., 1892, p. 229.

<sup>8</sup> Ann. Mus. civ. Genova (2), xix. p. 60 et seq.

<sup>&</sup>lt;sup>9</sup> Journ. Linn. Soc., xxvi. p. 198 et seq.

<sup>&</sup>lt;sup>10</sup> P. Z. S., 1886, p. 299.

<sup>&</sup>lt;sup>11</sup> Nouv. Arch. du Mus., 1872, p. 85.

<sup>&</sup>lt;sup>12</sup> Loc. cit., p. 168.

<sup>13</sup> Quart. Journ. Micr. Sci., xxix. 1889, p. 251.

<sup>14</sup> Rosa, Ann. Mus. civ. Genova (2), xix. p. 57.

I found myself obliged to abandon the task of attempting to distinguish these small Benhamias. One species from Lifu is a slender form with clitellum extending over segments XIII—XX with ornamented penial setae, a single oviducal pore and the usual internal characters. It is about 30—35 mm. long and appears to have no genital papillae. It is difficult to differentiate from or to identify with other small species.

There were many specimens of Pontodrilus from the Isle of Pines in the Loyalty

group.

It is clear therefore, that, as far as our present knowledge goes, the prevailing earthworm genus of this part of the world is *Perichaeta*. Out of a total of sixteen species known with certainty as recognisable species found within this region and not obviously (?) imported forms—like *Perichaeta indica* and *Eudrilus eugeniae*—no less than thirteen are *Perichaetas*. But nothing further can be said in favour of a Polynesian region, such as Mr Lydekker urges, from the point of view of earthworms. So far as earthworms are concerned there is, it appears to me, a great Oriental region which embraces Australia and Polynesia on the one hand, and the whole of the Malay Archipelago and India on the other. This cannot be profitably subdivided.

#### PERICHAETA NOVAE-BRITANNIAE, Benham.

P. novae-britannicae, Benham, Journ. Linn. Soc. Zool., xxvi. p. 199.

Dr Benham has given a very full account of the anatomy of this species; and I have practically nothing to add to his account. It is clearly the commonest species of New Britain, judging by the numbers contained in Dr Willey's collection. Dr Benham's figure of the papillae in the neighbourhood of the male pores does not however seem to me to exhibit their characters accurately. They are not glandular looking areas as are generally the copulatory papillae of these worms. In the specimens which I examined they were invariably sharp depressions in the body-wall (Fig. 9), looking as if they played the part of suckers rather than adhesive papillae. I may also observe that the species grows to a larger size than might be inferred from Benham's description. I have examined a well preserved example of 160 mm. by 8 mm. in breadth.

## PERICHAETA SEDGWICKII, Benham.

P. sedgwickii, Benham, loc. cit., p. 201.

Dr Benham described an exceedingly remarkable character in this species. Instead of the two normal caeca of *Perichaeta*, wanting in so few species, and placed always, or in the vast preponderance of species, in the XXVII or XXVII th segment, Benham

has mentioned in this species a single caecum placed rather further forward. This is, as I believe, an absolutely unique character in this genus. I was therefore particularly careful to endeavour to confirm or to deny Benham's statements. I may say that I found this single unpaired caecum in three specimens which I thought sufficient to dissect for the purpose; there can therefore I think be no doubt that we have here a genuine specific character and not a mere abnormality as might be suggested. The single caecum is in its characters precisely like one of the two caeca where there are two. It has the same somewhat crinkled aspect that the caeca of *Perichaeta* possess; and it is not unusually large so as to suggest a fusion between a medianly approximated pair.

One fact in the structure of this species has been apparently overlooked by Benham. He does not refer to the existence of genital papillae except a pair on either side of the male pores. These papillae (Fig. 3) are by no means always distinct; but in one of the individuals which I studied were quite obvious although forming somewhat faint impressions upon the body-wall. These papillae, though faintly outlined, are very large and occupy nearly the whole of the available space on the ventral side of the body. They occur both in the neighbourhood of the male pores and of the spermathecae. On each of segments XVII, XIX, XX, XXI, are a pair closely approximated to each other on the ventral surface of those segments, in front of the line of setae. In addition to these the XVIth to the XXth segments possess a pair of papillae situated to the outside of the set that has just been described. These latter are in fact on a line with the male pores. These papillae lie partly behind and partly in front of the setae of their respective segments, overlapping them in front. Those of the XVIIth and XVIIIth segments are more intersegmental in position, extending in each case a little way on to the following segment; they remind one much of the articular surfaces for ribs on two adjacent vertebral centra. It is these papillae only that Benham has referred to in his account of Perichaeta sedqwickii. The papillae in the neighbourhood of the spermathecal pores are placed on segments X-XIII. On each of these segments are a pair of ventrally placed papillae lying in front of the row of setae.

The other characters of the worms that I refer to *Perichaeta sedgwickii* agree so absolutely with the description given by Benham that I cannot doubt that they are specifically identical. Here however is a character, not always obvious, that when missing or apparently missing might have easily led to the creation of a new species, if but one example had been under observation.

#### PERICHAETA MALAMANIENSIS, Benham.

P. malamaniensis, Benham, loc. cit., p. 213.

Dr Benham's two species *Perichaeta arturi* and *P. malamaniensis* evidently come very close together. They agree to differ from all species of which at any rate we have adequate knowledge by the existence of a complex copulatory apparatus, which

<sup>&</sup>lt;sup>1</sup> The outer papillae of segment XVII are not visible in the specimen figured.

seems to be a further specialisation of a terminal sac of varying size into which the duct of the spermiducal gland opens in many other species. In fact we have in this genus an interesting series of stages in the evolution or degradation of this organ. In many species the duct of the spermiducal gland opens directly on to the exterior, in some cases not even widening before its aperture; in other cases it gets wider towards the external pore. The next stage is seen where the duct opens into a small sac before opening on to the exterior; in other species again this sac is larger and larger; and finally we have the two forms under consideration in which the sac exists, is large and is furnished with a protrusible or eversible penis. These two species furthermore agree in the fact that the spermiducal gland is bi- or even trilobed, each division then having its own separate duct. It does not seem to me to be very plain that there is much difference in the copulatory apparatus of P. arturi and P. malamaniensis. But one point of difference is noted by Benham and that is the form of the spermathecal appendix. In P. arturi it is long, longer than the main pouch, while it is small in P. malamaniensis. For this latter reason I refer examples of a worm which is certainly either one species or the other to P. malamaniensis; they were collected in New Britain on Gazelle Peninsula, on the Isle of Pines (New Caledonia), at Lifu and at Mare in the Loyalty Islands, and finally at Esafate in the New Hebrides. The original description of P. malamaniensis is of specimens from the Philippines.

#### PERICHAETA LORIAE, Rosa.

P. loriae, Rosa. Ann. Mus. civ. Genova (2), XIX. p. 61.

This form was described by Rosa from New Guinea. I have seen two examples from Guadalcanar in the Solomons. I have only to add to Dr Rosa's account that in one at any rate of these two individuals there were no setae on segments XIV and XV. In the other I observed them upon XV. In both examples there are setae upon segment XVI; but the glandular modification of the integument does not extend so far as the seta row.

### PERICHAETA UPOLUENSIS, F. E. B.

P. upoluensis, Beddard. Proc. Roy. Soc. Edinb., xiv. p. 174.

Nearly twelve years ago I described from Upolu in the Samoa group of Islands a *Perichaeta* which I believed, and believe, to be a distinct form. The species was mainly characterised by the character and distribution of the genital papillae. Dr Willey collected four examples of this same species at Esafate or Sandwich Island in the New Hebrides group. Distant though this Island is from Upolu, I consider w.

that we have to do with the same species. I cannot, after carefully comparing the new specimen with those from Upolu (one entire specimen I fortunately possess), see the slightest reason for separating them, although as will be seen I am able to add some details to my original account of this *Perichaeta*. *Perichaeta upoluensis* is a species which varies considerably in size. The largest of the examples collected by Dr Willey measures 166 mm. in length and consists of about 110 segments. The smallest example, but equally mature as regards the development of its sexual organs, is only 92 mm. in length and consists of but 95 segments.

This worm is characterised by a purplish tinge upon the dorsal surface. The dorsal pores commence between segments X and XI.

As I have already mentioned, the most characteristic feature of this species is the number and arrangement of the copulatory papillae. These show some variation from specimen to specimen, with of course the same general disposition. The papillae are in every case very small contrasting with those, for example, of *Perichaeta sedgwickii* just described.

Their characteristic feature (Fig. 2) is that a number of segments immediately following the clitellum have a single median papilla. They are not paired. I shall now describe the arrangement of the papillae in detail in the four specimens; this is by no means a waste of time or space, since species of *Perichaeta* are occasionally mainly or even entirely to be discriminated by the number and the arrangement of their papillae. And since furthermore some species have been described as to these organs from a single example. It is highly important therefore to take note of the variations which these structures exhibit. From a detailed account of the variations a general notion of the characteristics of the species can be obtained.

In one specimen there is a single papilla on each of segments X, XVII—XXI; and in addition to these median papillae two near to each male pore. One of these lies to the inside and above the pore, the other to the outside. In a second specimen there is no papilla upon segment X. But the median papillae in the neighbourhood of the male pores are increased by an additional one upon segment XXII. Moreover that upon segment XXI was double. The two papillae close to the male pores are increased in this individual to three.

In specimen No. 3 I did not detect a papilla upon segment X. But there were six on the segments following the clitellum, i.e. on XVII to XXII. A triangle of a papillae surrounded each male pore.

In the largest individual of this species there are only five papillae of the median series, thus showing that it is not always possible to assume that the largest individuals are more completely mature than smaller specimens. There was no papillae on X and only two in the immediate neighbourhood of the male pores. In my original account of this species I described a median papilla upon segment IX not upon segment X, as in one of the individuals collected by Dr Willey. It occurred to me that I might easily have made a mistake, and fortunately I have by me one of the specimens from which that description was compiled. I find on re-examination that I did not fall into an error in this matter.

The clitellum fully occupies segments XIV—XVI. I could not find any setae upon it.

As to the setae of this species they do not differ markedly in size on different segments of the body or on different parts of the same segment. Their numbers on certain segments are as follows:

X, 46; XIII, 50; XVII, 55; XXV, 54.

I counted 7 setae between the male pores.

As to the internal structure of this species of Perichaeta, the following facts appeared to me to be specially noteworthy.

There are five stoutish septa lying behind the gizzard, the last of which separates segments XIV and XV.

The last of the contractile "hearts" lies in segment XIII.

The gizzard is large and appears to lie in segments VIII, IX; I could find no septum separating these segments. The intestine begins in segment XVI. The caeca arise in XXVI and extend forward through three segments.

In the region of the intestine I found numerous racemose "lymph glands," lying as usual on either side of the dorsal vessel.

The reproductive organs are upon the usual plan. Two pairs of sperm sacs lie in segments XI and XII. The two of each side of the body are connected by a sperm reservoir, which projects into the tenth segment, and encloses the funnels of the sperm ducts. The two sperm reservoirs seem to be quite distinct, and between them runs the nerve cord. Corresponding to the sperm sacs are two comparatively large egg sacs in the XIVth segment. The large size of these structures in Perichaeta is often noticeable; but they have not been recorded in all species. In Perichaeta upoluensis they are of an elongate pear-shaped form. The spermathecae (Fig. 8) are present to the number of two pairs lying in segments VIII and IX. Each has a single diverticulum, which is longer than the pouch of which it is an appendix. The diverticulum is plainly divided into a region for the storage of the sperm and a duct. The extreme end of the diverticulum is again divided by a constriction and is dilated; this however is possibly only a temporary condition caused by the presence in it of abundant sperm. The spermiducal gland lies in three segments in front of its external orifice. The duct is unprovided with a terminal sac.

#### PERICHAETA ESAFATAE, n. sp.

One example of this, which I regard as a new species, was collected on the island of Esafate in the New Hebrides. As there is but this one specimen, my account of the species will have to be less complete than is desirable.

The worm measures 115 mm. and consists of 105 segments.

The colour dorsally is purple.

The clitellum occupies the usual segments and is devoid of setae.

The most characteristic feature of this species, as is so often the case in the genus *Perichaeta*, is the arrangement of the genital papillae. These are numerous in

the neighbourhood of the male pores and suggest those of *Perichaeta papulosa*<sup>1</sup>. The papillae are small sucker-like structures like those of *Perichaeta upoluensis*, not large flat papillae like those of *P. sedgwickii*. They have the following arrangement. On segment XVII are a pair lying side by side and close to the anterior boundary of the segment. Exactly corresponding to these in position are a pair on each of segments XVIII and XIX. On the border line of segments XVIII and XVIII (this boundary line is not marked on the ventral side of the body) are two papillae on each side, and to the outside of, and wider apart from each other than are the median papillae already spoken of. Two papillae lie just to the inside of each male pore one above the other, and finally a papilla lies to the outside of and in line with the male pore.

The male pores are not near together; but there appear to be only four setae between them; these however do not occupy the entire space between those pores but lie in the middle of the area.

The gizzard has the form of a truncated cone, being narrower anteriorly than posteriorly. Caeca are present.

Two particularly strong septa follow the gizzard, enclosing between them the XIth segment.

The last hearts are in segment XIII.

The sperm sacs lying in XI, XII are unusually small, not very much larger indeed than the egg sacs in XIV. The spermiducal glands lie in segments XVII, XVIII, XIX; they are rather bean-shaped and not greatly broken up into lobes and lobules. From the hilum runs the short stout duct unprovided with any terminal sac. The spermathecae are two pairs in VIII and IX; the diverticulum is long and stout, and those of the anterior pair lie in the VIIth segment. The diverticulum has a distinct duct and is longer than the pouch.

#### PERICHAETA SOLOMONIS, n. sp.

Of this rather large new species of *Perichaeta* the collection contained two examples from Narowol, Solomon Islands, and a third specimen from Rubiana, New Georgia, Solomon Islands.

The species is of a rich brown colour, becoming purple on the dorsal surface anteriorly; whitish lines mark the implantation of the setae.

The largest specimen measures about 140 mm, in length by 9 mm, in greatest breadth; it consists of 90 segments.

The clitellum is not that of typical *Perichaetae*. In the larger specimen it embraces only half of the XIVth segment, the XVth and the XVIth. There is a complete circle of setae on segment XVI. In the second specimen from Narowol the clitellum is more restricted still; it occupies only half of XIV and the whole of XV.

The genital papillae (Fig. 1) are numerous and characteristic. But here again, as is so very usually the case, there is some variation from individual to individual. In all

<sup>&</sup>lt;sup>1</sup> Rosa, I lombrichi raccolti in Sumatra, Ann. Mus. civ. Genova (2), xvi. p. 525.

specimens papillae exist near to the spermathecal pores as well as in the neighbour-hood of the male pores. In the larger example, whose measurements are given above, the arrangement was this:—On segment XIX there are three papillae lying side by side in the middle of the segment, a little in front of the line of setae. In the two following segments there are, on each, five papillae, one on each side being added to the three of the XIXth segment. On the XXIInd segment only two of these five were visible, those on the outside (left side). The anterior sets of papillae lie on segments X, XI; on the Xth segment there is a row of four papillae and six on the XIth; these papillae lie in every case in front of the setae of their segments.

In the smaller individual from Narowol each of segments XIX—XXI has a symmetrical row of four papillae. Those upon segments X, XI are fewer and not symmetrical; there are three on the latter and four on the former.

In the specimen of *Perichaeta solomonis* from New Georgia, the disposition of the papillae was a little different. On each of segments XIX—XXII were four symmetrically placed papillae, save on the last of these segments where one was missing. There were also two or three papillae on segments X and XI.

The porophores bearing the male pores are very conspicuous in this species. They are much raised and of a whitish colour. The actual male pore is in the line of setae, and the two are separated by a line of fifteen setae. Anteriorly to each pore is a sucker-like papilla.

This is a stout and strong species of *Perichaeta*; corresponding to these characteristics the septa and the muscular development generally within the body-cavity is pronounced. Behind the gizzard are five rather stout septa which are to some extent tied together by muscular bands. From the posterior as well as from the anterior margin of the gizzard itself arise half a dozen broadish muscular bands which bind it to the following septum or to the body-wall. From the pharynx radiate out a large number of slips of muscle which for the most part perforate adjacent septa and are inserted on to the body-wall. It is interesting to notice that the septum separating segments VIII and IX is present and is indeed moderately stout. In so many cases this septum has been recorded as absent that there can be little doubt that it is not always represented; but in one or two species its existence has been mentioned by several authors. Benham, for example, has especially noted its presence in *Perichaeta arturi*. The bulk of the gizzard in *Perichaeta solomonis* lies in front of the septum and belongs therefore to segment VIII. I find in this species, as did Benham in *P. arturi*, a pair of hearts corresponding to this segment. The intestine has caeca.

The most noteworthy point about the vascular system that I observed was the fact that the last pair of hearts are in the XIIth segment and not, as is so generally the case, in segment XIII.

Perichaeta solomonis is also remarkable for the fact that it possesses three pairs of sperm-sacs instead of the more usual two. These lie in segments X—XII; they are large, and the first pair are racemose in appearance. The egg-sacs in the XIVth segment are large and conspicuous. The spermiducal glands (Fig. 6) are cut transversely into three lobes lying respectively in segments XVIII, XIX, XX; each lobe is again

<sup>1</sup> I also describe it here in P. pacifica (p. 191).

subdivided more coarsely and then more finely. The ultimate lobules are very minute. The duct of the gland, which is unprovided with a terminal sac, arises from the posterior margin of the anterior of the three lobes. The spermathecae (Fig. 5) are five pairs in segments V—IX. They are pear-shaped with a longish but narrow diverticulum which is about half the length of the pouch.

In the same tube which contained the worms from Narowol were a number of smaller worms, of which two were larger than the rest, and mature. In spite of the superficial likenesses of these to the ones that have just been described, I was at first disposed to place them in a different species on account of their smaller size. They are slender worms, the largest being 113 mm. long with a diameter of 3—4 mm. The number of segments in this specimen was 100. The colour is the same as in the typical *Perichaeta solomonis*. The genital papillae, however, differ in detail. But they present a general similarity of arrangement. In the larger of the two specimens now under consideration the papillae were fewer than in the smaller individual. In the latter are a pair of papillae on each of segments XVII—XIX, corresponding in position to the male pores. The XIXth has in addition a median papilla and on segment XVIII are a pair of such papillae.

On segment IX there are three median papillae. The clitellum is rather defective, occupying segments XIV—XVI, and setae are present on the first and last of these segments. The internal organs correspond in every detail to those of the typical Perichaeta solomonis save that the muscular bands tying the gizzard to the parietes are wanting.

Is this to be regarded as a dwarf variety which, on account of its small size, has not area sufficient for the development of the full complement of papillae? I am inclined not to take this view, and mainly for the following reasons. Among the smaller worms contained in the tube were two or three which I consider to be immature forms of the typical Perichaeta solomonis. It is of course impossible to be certain upon this point; their very immaturity is in the way of arriving at a definite conclusion. Now these presumed immature forms of the typical Perichaeta solomonis have the robust form of the type and not the slender form of the variety which I am now considering. There would seem therefore to be more difference between the two varieties than a mere precocious development of the sexual organs. Yet the close similarity of colour and the identity of internal structure must be borne in mind in coming to a conclusion. I am inclined to look upon these slender examples of the typical Perichaeta solomonis as individuals which represent a new species in the course of differentiation; the modification has advanced to a certain extent in certain of the external characteristics but has not yet touched the internal organs.

#### PERICHAETA PACIFICA, n. sp.

Dr Willey's collection contains a considerable number of examples of a small *Perichaeta* which I refer to a new species.

One of these specimens was much larger than the rest, which were all small.

This example measures 56 mm. in length and consists of some 90 segments; of the remaining specimens the largest was not more than 38 mm. in length. The smaller specimens were all collected on the banks of a rivulet in New Britain; the largest example bears the label "Gazelle Peninsula, New Britain."

This species of *Perichaeta* is coloured above of a bluish violet tint. My observations upon the species chiefly relate to some of the smaller specimens which I examined as to external characters as microscopical objects and by longitudinal sections. But the largest specimen was dissected and was found to differ in no point of importance that I could ascertain from the smaller individuals save in the number of the genital papillae. These papillae (Fig. 4) differ somewhat from individual to individual and the largest number were not present in the largest specimen. In that specimen their arrangement was as follows:—On each of segments XX—XXII there was a long transversely elongated papilla median in position and unpaired. In a smaller example the same papillae were present and in addition one upon each of segments XVII and XVIII as well as upon XII and XIII.

The clitellum occupies segments XIV—XVI; the last segment appears to always possess a complete circle of setae at the margin where the glandular development of the segment ends; in the large specimen the XVth segment also had a complete circle of setae. In a smaller individual mounted as a microscopic object I could see no setae upon the XVth segment; but in addition to those upon the XVIth were three setae on each side of the oviducal pore upon the XIVth.

In this latter specimen the setae upon a selected series of segments were present in the following numbers: VIII, 37; XIII, 47; XVII, 46.

There are in this specimen 10 setae between the male pores.

The septa dividing segments VII and VIII are thick; but those dividing segments IX and X are especially thickened. They are the thickest septa of all. Contrary to what is apparently sometimes found in this genus the septum between segments VIII and IX was present, though thin. In sections which did not embrace the gizzard this septum was seen to lie straight across the body-cavity and to bound a space—the coelom of the VIIIth segment—very much less than that bounded by the thick septum immediately following it. But in sections in which the gizzard was shown in position the septum was convex backwards so that the gizzard chiefly lies in the VIIIth segment.

Caeca are present. The last "hearts" are in segment XII.

The reproductive organs are mainly remarkable for the fact that there is but a single pair of testes, sperm ducts and sperm sacs. The testes lie together with the funnels lying opposite to them in a special sac, the sperm reservoir. The single pair of sperm sacs are in segment XII. They are racemose in appearance. The spermiducal glands extend through three segments, i.e. XVII—XIX. The duct is short and has no terminal sac. The spermathecae are present to the number of four pairs in segment VI—IX. Each has a single tubular diverticulum. It seemed to me that the sperm duct did not open into the duct of the spermiducal gland until a little way in front of the external aperture of the latter. Dr Benham has found the same state of affairs to characterise *P. malamaniensis* and quotes my own discovery of the union between the male duct and the duct of the spermiducal gland at a late point

in P. perkinsi<sup>1</sup>. He suggests that this may not be an unusual occurrence in the genus Perichaeta. It is at any rate not universal, for I have examined from this point of view the Bermudan species P. bermudensis in which I find that the sperm ducts open into the duct of the spermiducal gland before it acquires its thick muscular coat.

The most salient structural feature of this Perichaeta is the presence of only a single pair of sperm sacs to which correspond but a single pair of testes and sperm ducts. Dr Rosa has pointed out that at present this character—the possession of only a single pair of sperm sacs—characterises nearly all the species of the genus from New Zealand. It is to be seen in P. forbesi, F. E. B., P. neoguinensis, Mich., and in P. loriae and P. papua of Rosa. In a specimen of Perichaeta however, not identified, from New Guinea, Rosa did not find that characteristic feature; that Perichaeta had the usual two pairs of sperm sacs. It is therefore important clearly to distinguish the present species, which is not widely separated in geographical range from any of those forms. It will be apparent I trust from the foregoing description that Perichaeta pacifica cannot be confounded with any of the above mentioned species. I imagine that it will be found when those species are more fully investigated that they will prove like P. pacifica to possess only a single pair of testes and funnels.

#### PONTODRILUS MATSUSHIMENSIS, Iizuka.

P. matsushimensis, Iizuka, Annotationes Zool. Japon. II., Pt. i., p. 21.

Dr Willey collected a large number of a species of *Pontodrilus* on the shore of the Isle of Pines which I identify with the above named species of the genus. That species is a native of the Japanese shores, having been met with there and described by Akira Iizuka. The fulness of Mr Iizuka's description renders it unnecessary for me to give an attempt at a complete account of the characters of the worm; but there are some points about the species which require a few notes.

The describer of the species does not comment upon the setae—as to whether they are or are not ornamented. This character is known to distinguish one species of the genus, viz. P. bermudensis<sup>2</sup>. I do not find any ornamentation; for this reason and for the fact that the thickened septa extend from segments V to XIII, the present form from the Isle of Pines cannot be the same as P. bermudensis. In the latter species the thickened septa extend from segments IV to XI.

In my specimens however the clitellum is not quite so extensive as it is described to be by Iizuka. He states that it comprises segments XII—XVII; but in the plate it is represented as extending over segments XIII—XVII only (the oviducal pores being wrongly assigned to segment XIII). This is precisely what I found in Dr Willey's examples. Furthermore the oviducal pores lie a little to the inside and

<sup>&</sup>lt;sup>1</sup> On some Earthworms from the Sandwich Islands, &c., P. Z. S., 1896, p. 200.

<sup>&</sup>lt;sup>2</sup> Pontodrilus arenae of Michaelsen: Terricolen der Berliner Zoologischen Sammlung, Arch. f. Naturg., 1892.

of course in front of the innermost of the setae. Like the describer of the species I could find no setae near to the male pores; in that segment (the XVIIIth) the inner pair of setae are wanting.

Iizuka found that in this species the sperm ducts do not open at the junction between the muscular and glandular parts of the spermiducal gland. He remarks further that "the exact relation of the vas deferens and the spermiducal gland in Pontodrilus has probably never been subjected to careful examination by means of serial sections." I cannot recollect whether my own statement, which he quotes as part of the generic definition of the genus Pontodrilus, was based on actual examination; but I imagine that it was, since the figures of Perrier would naturally not be conclusive upon the point. In any case I have re-examined Pontodrilus littoralis and find that the sperm duct does joint the spermiducal gland at the junction of the glandular part with the muscular duct. I endeavoured to ascertain how far Pontodrilus hesperidum agreed with the type species in this particular, but without effect. The variability in this matter is precisely analogous to that which is found in certain species of Perichaeta and which has been referred to above under the description of Perichaeta pacifica. In some the sperm duct joins the spermiducal gland higher up than in others. The fact is evidently of no great importance; but it is clear that it must be removed from the generic definition of Pontodrilus.

#### DESCRIPTION OF PLATE XXI.

- Fig. 1. Perichaeta solomonis: ventral surface of anterior segments.
  - " 2. Perichaeta upoluensis " "
- " 3. Perichaeta sedgwickii " ",
- " 4. Perichaeta pacifica " "
- " 5. P. solomonis: spermatheca.
- ,, 6. , spermiducal gland.
- ,, 7. P. upoluensis: spermiducal gland.
- ,, 8. ,, spermatheca.
- " 9. P. novae-britanniae: ventral surface of segments XIII—XIX.

Note. To facilitate comparison it may be repeated here that the clitellum, in all the species figured, occupies segments XIV—XVI. The female orifice lies in the middle of segment XIV, and the paired male orifices occur on segment XVIII. One of the chief objects of the external views is to illustrate the appearance and distribution of the **copulatory papillae** which, as described in the text, are subject to considerable individual variation.



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#### THE GORGONACEA COLLECTED BY DR WILLEY.

By ISA L. HILES, B.Sc. (VICT.), OWENS COLLEGE, MANCHESTER.

#### With Plates XXII—XXIII.

This collection of Gorgonacea has proved a very interesting one, including several new forms. One new species has been added to that little known genus Keroeides; there is one new species each of Acamptogorgia; of Acanthogorgia; of Villogorgia; and of Chrysogorgia.

My thanks are due to Professor Bell for the trouble he took to help me in

comparing some of the specimens with those in the National Collection.

Professor Hickson has very kindly given me much help, especially with regard to the literature bearing on the group. The classification adopted is that laid down by Wright and Studer in the Challenger Report on Alcyonaria (6).

#### SECTION. HOLAXONIA.

FAMILY. DASYGORGIDAE.

Sub-family. Chrysogorgidae.

Chrysogorgia constricta, n. sp. (Pl. XXII. Figs. 8, 9, 10.)

There is only one fragment of this species 205 mm. in length. It gives off two branches, one 75 mm. in length which bears a small lateral branchlet, and the other 70 mm, above the first and 43 mm, long. The stem is 1.5 mm, in diameter at the lowest point; the basal part is missing.

The axis is horny with calcareous particles scattered in broken rings.

coenenchyma is thin.

The polyps are large, directed obliquely upwards; they are distinctly divided into two regions by a constriction. The lower region measures 4 mm. high by 3 mm. in diameter where attached; the upper part measures 2.5 mm. by 1.5 mm. in diameter. The whole polyp is thus 6.5 mm. high. The polyps arise alternately on the two sides of the axis at intervals of 9 or 10 mm. The branches bear, close to the apex, two polyps, one slightly in advance of the other, and between them is a blunt projection, the actual apex of the branch.

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The spicules are spindles with a few blunt spines. Some are long and broad and have only 1 or 2 spines, but these are rare. On the polyps they are arranged en chevron in 8 ascending rows, and the polyp is distinctly divided into 8 lobes which are continuations of the ridges formed by the rows of spicules. There are no spicules transversely arranged either in the upper or the lower part of the polyp. The colour in spirit is white. The axis is yellow.

This species differs from *Chrysogorgia desbonni*, Duchassaing and Michelotti (1), in the position and shape of the calyces and in the arrangement of the spicules in the lower portion of the calyces, where they are not transversely placed. It differs in the same point from *Chrysogorgia fewkesii*, Verrill (3).

Habitat. Talili Bay, New Britain.

#### FAMILY. ISIDAE.

Sub-family. MOPSEINAE.

Primnoisis ambigua, Wright and Studer. (Pl. XXII. Fig. 11.)

Only two very small colonies have been preserved. The axis shows fairly short, calcareous joints, cylindrical and longitudinally fluted.

The ends of the twigs are formed by a short, calcareous joint.

In the stem and branches the calcareous joints are 2.2 mm. in length and the horny joints 12 mm. Thus both are much smaller than in the Challenger specimen. But the calcareous joints are larger in proportion than the horny joints.

The diameter of the axis is 2 mm.

The branches are given off from the calcareous joints, but rather irregularly, some of the joints bearing no branches. They spring from a small, calcareous projection, followed by a horny joint.

The spicules are longish, with strongly toothed edges. In the calyces the spicules are transversely placed, with sharp teeth on the margin which interlock with those of the next plate.

The spicules vary in size, some being '18 mm.  $\log \times$  '13 mm. in diameter, others '16  $\times$  '08 mm., and others again '12  $\times$  '02 mm.

The spicules are therefore somewhat smaller than those of the type specimen, Wright and Studer (6), which measure  $28 \times 1$  mm.— $17 \times 05$  mm.

The coenenchyma is thin and transparent and preserved only in patches.

The club-shaped polyps are fairly numerous on the twigs and directed obliquely upwards; they measure '6—'7 mm. in height and are about '6 mm. apart. In the type specimen they are '8—1 mm. high.

The calcareous and horny joints in the specimen in the Challenger collection measure 2:5—4 mm. and :5—1 mm. respectively. Thus the proportionate lengths differ.

These fragments differ from the type specimen in three small points of measurement, differences which are not of sufficient importance to justify a new species.

Habitat. Sandal Bay, Lifu.

Previously recorded from Kerguelen Island. Depth, 10-80 fathoms.

#### FAMILY. MURICEIDAE.

Acamptogorgia acanthostoma, Germanos.

This fragment agrees with Germanos' description (8) of a colony from Ternate except as regards the colour, which is not whitish but greyish brown.

The centre of the axis is divided into chambers and many of the chambers contain calcareous matter in the form of irregular lumps,

The spicules are decidedly larger than in the form described by Germanos, in which they measure 15 mm. and 25 mm. In this form on the average they measure 5 × 4 mm. Otherwise it agrees with Germanos' description and excellent figures.

Habitat. Milne Bay, British New Guinea. About 20 fathoms.

Previously recorded from Ternate.

Acamptogorgia spinosa, Hiles1.

The specimens consist of two fragments, the larger of which measures 95 mm. in height and 70 mm. across the broadest part. It is evidently only the fragment of a larger colony, as there is no basal part and no branch which could be called the main stem. The thickest branches measure '5 mm. in diameter. It resembles the specimen Acamptogorgia spinosa from Funafuti except that it is somewhat darker in colour and larger generally. This may be due to the specimens being fragments from an older colony. The calyx spicules also project slightly further.

#### Measurements.

|                       | $Funafuti\ specimen.$                  | These fragments.                       |
|-----------------------|--|--|
| Polyps.               | ·73 mm. high.                          | ·83 mm. high.                          |
| 27                    | 55 mm. in diameter at the base.        | ·86 mm. at the base.                   |
| Opercular spicules.   | $36 \text{ mm.} \times 09 \text{ mm.}$ | '55 mm. $\times$ '18 mm.               |
| Polyp spicules.       | 37 mm. × 36 mm.                        | 66 mm. $\times$ 44 mm.                 |
| Coenenchyma spicules. | '11 mm. × '31 mm.                      | $36 \text{ mm.} \times 47 \text{ mm.}$ |

The spicules are thus larger; still these differences do not seem to justify making a new species. Both forms are from the same depth.

Habitat. Blanche Bay, New Britain. 40 fathoms.

Recorded from Funafuti, Ellice Islands.

Acamptogorgia tuberculata, n. sp. (Pl. XXII. Figs. 1 and 2.)

There is one small colony of this species. The main stem is 32 mm. in height by 1.4 mm. in diameter near the base.

It gives off branches on the two sides in the same plane, 6 branches altogether. Three of these bear each a lateral branch.

The longest branch is 20 mm. in length. The polyps are closely placed on three sides of the stem and branches, leaving the back of the branches free.

<sup>1</sup> My account of the Gorgonacea collected by Mr J. Stanley Gardiner in Funafuti will be presented to the Zoological Society on January 17th, 1899.

Each branch bears at the apex two laterally placed polyps.

The polyps are low and cylindrical in shape; they measure 1.5 mm. by 1.4 mm.

The axis is horny, brown in the older parts, white at the apices.

The coenenchyma is fairly thin and both it and the calyces are very rough, looking "lumpy" owing to the projecting foliar expansions of the spicules.

The operculum is low and conical.

The spicules of the coenenchyma and polyps are alike; they are slightly bent spindles, with spiny warts along one side, and on the convex side at one end or about the middle arise complex foliar prominences. They measure  $51 \times 18$  mm.,  $36 \times 33$  mm.,  $42 \times 14$  mm.; the foliar expansion measures about  $18 - 25 \times 16$  mm.

The spicules of the collaret are curved spindles with a few spines; they measure  $\cdot 27 \times \cdot 034$  mm.

The opercular spicules are flat, spiny, more pointed at one end than the other; they measure  $30 \times 054$  mm. There are eight groups of three spicules.

The spicules are all colourless.

The coenenchyma and polyps are white.

The spicules resemble closely in form and in size those of A. fruticosa, Germanos, from Ternate, but that species is dark red in colour.

But the polyp calyces are much larger than those of A. fruticosa, and the surface of the colony is more closely crowded with prominences from the spicules, hence I have suggested the name of Acamptogorgia tuberculata.

Acanthogorgia spinosa, n. sp. (Pl. XXII. Figs. 3-6.)

There are four fragments, the largest of which measures 135 mm. long and is evidently only the end of a branch. It bears three branches on one side of the axis, at intervals of 20 and 35 mm., and one in a plane at right angles to the others at a further interval of 46 mm. and within 35 mm. of the tip.

Two of these branches bear each a small branch of the third order.

The main branch measures 2 mm. in diameter at the lower end.

The coenenchyma is thin and fairly smooth.

The axis is horny and brown in colour.

The polyps arise from all sides of the stem and branches, and are closely crowded together. The apices of the branch and twigs are occupied by a polyp.

In shape the polyps are elongated, cylindrical and somewhat expanded at the summit. They are placed perpendicularly on the branches; they measure from 3—4 mm. in length, '9 mm. in breadth at the base, and 1.3 mm. across the crown. The polyps are thickly crowded round the branches.

The spicules of the coenenchyma are chiefly of the quadri-radiate type, measuring  $26 \times 16$  mm., but longish spindles with small scattered spines, measuring  $7 \times 07$ — $11 \times 01$  mm. length by breadth, also occur.

In the polyps the spicules form eight longitudinal rows; each consists of two sets of spicules arranged *en chevron*, which are continued to the bases of the tentacles.

At the top of these rows are the long bundles of spicules (each consisting of

2 or 3 needles) which project above the polyp head for some distance, having only a small portion of the lower end embedded in the calyx.

These spicules are all of the same type—spindles—bent at the lower end which bears only a few, scattered, small spines in the projecting spicules, those of the calyx-wall being more or less covered with them.

The projecting spicules measure  $1.4 \text{ mm.} \times 1 \text{ mm.}$ ; those of the polyp-wall measure  $5 \times 0.4 \text{ mm.}$ 

The colour in alcohol is dirty white.

This form seems closely allied to Acanthogorgia muricata, Verrill, from Nova Scotia. In the size of the calyces it approaches more nearly A. muricata, Verrill, from the Barbadoes, where they are about 3 mm. high.

The only apparent difference from A. muricata is that there are 8 projecting groups of 2 or 3 spindles, while in A. muricata there are 8 single spicules; this is quite a sufficient distinction for a new species.

Habitat. Mouth of Blanche Bay, New Britain. Depth, 25 fathoms.

Villogorgia intricata, Gray.

The specimen is somewhat larger than that described in the Challenger Collection.

The base of the colony is missing, but the height of the portion present is

150 mm.; the width is about the same, but the colony is evidently imperfect.

The main branches measure 1 mm. in thickness and reach to the top of the colony.

The polyps are irregularly scattered round the stem at intervals of approximately 1 mm. They measure '48 mm. in height, by '55 mm. in breadth, thus agreeing with those of the Challenger specimen.

The spicules of the coenenchyma are 4-rayed stars, and spindles branched on one side.

The axis is horny, flexible, the centre hollow and divided into horizontal chambers; in some parts of the stem these are filled with calcareous matter in the form of irregular lumps.

The axis is light yellow in colour and the colony in spirits is brownish.

Habitat. Sandal Bay, Lifu. Depth 30 to 40 fathoms.

Previously recorded from Bass Straits, Fiji, and the New Hebrides.

Epizoic on this form are several specimens of an Ophiuroid which corresponds fairly well to Astroschema koehleri, Döderlein (10); the only differences are in the length of the arms in proportion to the width of the disc, which in these forms is as 12 mm. to 1.5 mm., and in Dr Döderlein's as 10.6 mm. to 2.3 mm., also the rings of warts on the upper surface of the arms are not apparent.

There are also specimens of the Mollusc Avicula hirundo attached to the colony.

Villogorgia rubra, Hiles.

There is one specimen which resembles closely the new species, Villogorgia rubra, described by me in the collection of Gorgonidae from Funafuti, Ellice Islands<sup>1</sup>.

<sup>1</sup> See footnote on p. 197.

The colony is upright and richly branched in one plane. The base is missing and the colony has the terminal branches somewhat broken.

The branches arise from both sides of the stem at an angle of from 80°—90°. The lateral twigs of the branches arise fairly perpendicularly.

Some bend after a short distance and run parallel with the parent branch.

The height of the colony is 70 mm., the greatest breadth 60 mm. The thickness of the principal stem at the base is 1 mm. The coenenchyma is thin.

On the branches the polyps are about 1 mm. apart, but on the main stem they are not so closely placed, being often 2 mm. apart. They are perpendicularly placed, chiefly on two sides of the stem and branches.

Habitat. Sandal Bay, Lifu.

Villogorgia compressa, n. sp. (Pl. XXII. Fig. 7.)

There is one very fine colony and one smaller piece.

The large colony measures 490 mm. high and 540 mm. across the broadest part; the basal part is missing.

The colony is richly branched in one plane, the branches springing from both sides of the stem at angles of from 80°—90°.

There are numerous anastomoses of big and small branches.

The thickest branches are almost ribbon-like, being flattened at right angles to the plane of branching. They measure 3 mm. by 1 mm. in diameter. The coenenchyma is thin.

The polyps are perpendicular to the stems and branches; they are rather less frequent on one face of the branches than the other.

They are fairly thick on the terminal branches, but elsewhere they occur at intervals of from 1-2 mm.

There are two polyps at the end of each branch, neither terminal.

They measure 1.2—1 mm. in height by 1.05—83 mm. in breadth across the crown.

The spicules are of the Villogorgia type (6) and measure:—the stellate forms of the cortex—15 mm. by '036 mm. (width of the main portion) and '027 mm. (width of the base of the rays); the fusiform spicules of the cortex—55 mm. × 05 mm.; the opercular spicules—36 mm. × 05 mm.; the polyp spicules—4 mm. × 17 mm.

These are maximum measurements in all cases.

The operculum is of the Villogorgia type.

The axis is horny, flexible, with the central core chambered.

The colour of the colony in spirit is dirty brown. The spicules are colourless.

This form differs from V. intricata in its size, being larger, and in the greater roughness of its appearance.

It differs from V. flabellata in form and in its spicules, from V. mauritiensis in the shape of the spicules, and from V. nigrescens in the size, &c. of the vertucae.

Habitat. Blanche Bay, New Britain. Depth, 50 fathoms.

<sup>&</sup>lt;sup>1</sup> In fresh condition the prevailing colour was pink due to the coloured zooids; the coenosarc had a brownish neutral tint.

#### SECTION. SCLERAXONIA.

#### FAMILY. SCLEROGORGIDAE.

Keroeides gracilis, Whitelegge. (Pl. XXII. Figs. 12-14.)

Only a few fragments of this form have been found. The largest closely approximates to that described by Whitelegge (9).

The verrucae alternate on the sides of the stem and branches. They are low and conical in shape, measuring 1 mm. in height and the same in diameter at the base.

On the main stem they are about 3 mm. apart, on the branches 1-2 mm. apart.

The coenenchyma is thin, smooth and filled with large, closely packed, compound tuberculated spindles.

The axis consists of a number of long, closely-set spicules cemented together round a horny central strand and agrees in diameter with the type specimen.

The irregularity in the shape of the coenenchyma spicules near the verrucae is not so apparent as Whitelegge describes it.

The spicules are pale pink in colour by transmitted light.

They are '84 mm. long and '27 mm. wide.

The small tentacular spicules are  $11 \times 04$  mm, and the spicules of the axis are  $22 \times 02$  mm.

Thus all the spicules are somewhat smaller than in K. gracilis, Whitelegge, where they are  $1 \times 15$  mm.  $-2 \times 3$  mm.

The colour of the colony also differs from that of K, gracilis, being pale pink instead of coral red; but they are both shallow water-forms.

I do not consider that these small points of difference are sufficient for characterising a new species, especially as there are only a few fragments of the specimen and no complete colony.

Habitat. Milne Bay, British New Guinea. Depth 20 fathoms.

Previously recorded from Funafuti, Ellice Islands.

Keroeides pallida, n. sp. (Pl. XXII. Figs. 15 and 16.)

There is one fairly complete specimen showing the basal attachment, and three fragments. The largest piece measures 130 mm. in height and 140 mm. across the widest part of the colony. The diameter of the main stem near the base is 40 mm. by 2.5 mm., and of the terminal branches 2.0 mm. by 1.0 mm. Thus both stem and branches are somewhat flattened. The main stem is broken off at a height of 85 mm-from the base.

The main stem gives off five branches in one plane at an angle of about 60°. They soon turn upwards and run parallel to the main stem. Each in its turn bears two or three branches, some of which also bear branchets. The branches end in two polyps. Originally the branching must have been in one plane; the curving inwards seems to be due to the position in the bottle of spirit.

The polyps are borne chiefly on the two sides, and, as a rule, alternately.

The verrucae are cylindrical in shape; in no case has the polyp completely retracted, the tentacles being visible.

The verrucae measure 1.5—2.0 mm. in height, and 1.5 mm. in diameter at the base. They are about 3 mm. apart.

The coenenchyma is thin and smooth, being filled with closely packed, multituberculate spindles. The spicules are all colourless.

The axis is sclerogorgic; dark brown in colour in the main stem and lighter brown in the branches.

The base of the colony consists of a flat, spreading disc.

The spicules measure 1.06 mm.  $\times$  27 mm. to '24 mm.  $\times$  04 mm.

The tentacular spicules measure  $23 \text{ mm.} \times 03 \text{ mm.}$  The spicules of the axis measure  $46 \text{ mm.} \times 24 \text{ mm.}$ 

The colony is pale fawn in colour.

The spicules resemble those of *Keroeides koreni*, Wright and Studer (6), from the Hyalonema ground off Japan, but the colour, size and general appearance of the colony separate the two forms. It differs also in the same features from *K. gracilis*, Whitelegge.

Habitat. Talili Bay, New Britain. Dredged in 30 fathoms.

#### FAMILY. GORGONELLIDAE.

Verrucella guadalupensis, Duchassaing and Michelotti. (Pl. XXIII. Figs. 1, 2.)

There is one large specimen and several small pieces which may be fragments of the large colony.

It is much branched in one plane, the branching being irregular sometimes opposite but generally alternate.

The colony measures 310 mm. in height and the main stem is 3.5 mm. thick at the base.

The colony was attached by a calcareous enlargement at the base.

The main stem gives off numerous thick branches, slightly less in diameter than the stem itself at the point of branching. Between these branches are numerous small twigs.

Each branch bears branches of the second order, which give off branches of the third order, and so on up to the fifth order. Anastomoses occur fairly frequently even between branches of the first order.

All the branches arise at angles of about 60°. The axis is hard, lamellar, calcified; it is pale yellow in colour.

The cortex is thin, smooth and friable, whitish in colour and appearing granulated under the lens.

There is no terminal polyp, the branches bearing two lateral, opposite polyps close to the end.

The verrucae are small and wart-like and are borne on all sides of the lower part of the main stem at fairly large intervals. On the upper part of the stem and on the branches they are borne chiefly laterally and alternately.

They measure 36 to 64 mm. in height, and 5 mm. in breadth.

The terminal ones are usually large, measuring '92 mm. by 1'01 mm. at the base. They are smooth, like the rest of the coenenchyma, and divided into eight rays at the summit, which are folded over the retracted polyps.

The spicules are double clubs and double spindles with irregular rings of tubercles and a bare zone in the centre.

Some are pointed at the ends and some are rounded. There are a few double stars.

The spicules are colourless.

The pointed spicules measure  $11 \times 018$  mm.

Those with rounded ends measure '08 × '036 mm.

The double stars measure  $0.46 \times 0.18$  mm.

The colony is pale fawn in colour in spirit. When alive it was pure white.

Habitat. Blanche Bay, New Britain. Depth, 50 fathoms.

Previously recorded from the West Indies. It is a noteworthy point in geographical distribution, that the same species of *Verrucella* should be found both in the West Indies and at a depth of 50 fathoms in Blanche Bay, New Britain.

Commensal with this species of Verrucella is a large number of Anemones, belonging apparently to the tribe Hexactiniae, family Amphianthidae Hertwig, all the members of which are attached to Gorgonidae.

The circular muscle, i.e. the sphincter, is mesogloeal and very powerful.

It is not a *Stephanactis*, as there is no circular swelling dividing the animal into an upper and a lower section, and the tentacles are not numerous, but the animals are all in such a strong state of contraction that it is impossible to accurately tell their number or arrangement.

It is not an Amphianthus, as the wall is not covered with papillae.

It agrees most closely with Gephyra dornii, v. Koch; the two forms are of the same size, 1.5 mm. in diameter at the base and 1 to 1.5 mm. in height. But the tentacles are less numerous, seeming to be in two rows of 18. Von Koch describes a secretion of horny matter of which I see no trace in this form. Thus the specimens do not seem to belong to any of the three known genera of the Amphianthidae. The characters, as far as it is possible to make them out owing to the strongly contracted condition, are:—

Amphianthidae with a firm, smooth wall and a strong circular muscle, mesogloeal in position; the tentacles are apparently in two rows of 18. There is no circular swelling.

Provisionally the name of *Peronanthus*<sup>2</sup> verrucellae might be given to these commensal anemones.

<sup>&</sup>lt;sup>1</sup> The tentacles, if they can be so called, were quite obscure in the fresh condition and the Anthozooid bore an external resemblance to a Scyphistoma. The colour was reddish yellow. [Ed.]

<sup>&</sup>lt;sup>2</sup> περόνη a brooch, and ανθος a flower.

#### FAMILY. MELITODIDAE.

#### Melitodes ochracea, Lamouroux.

There are specimens in three separate bottles, two fairly large colonies, and several fragments.

One of the larger ones measures 290 mm. high; the main stem at the lowest horny joint measures 8 mm., and the calcareous joint above it measures 3 mm.

The other colony is 260 mm. in height.

The colony is dark red in colour, smooth and showing marked jointing of the axis, as the measurements show.

The polyps, which are fairly well expanded, are green in colour.

Habitat. Talili Bay, New Britain.

Previously recorded from Singapore. Numerous specimens have been referred to in various publications, but unfortunately localities are not given.



HILES. GORGONA

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#### EXPLANATION OF PLATES XXII. AND XXIII.

#### PLATE XXII.

(Most of the drawings for this plate were made by the author.)

- Fig. 1. Acamptogorgia tuberculata, n. sp. Colony. × 2.
- Fig. 2. Spicules of same.
- Fig. 3. Acanthogorgia spinosa, n. sp. Polyp-head.
- Fig. 4. Spicules of same; (a) of the operculum, (b) of the polyp, (c) of the coenenchyma.
- Fig. 5. Acanthogorgia spinosa. End of branch of a decalcified portion of colony. × 3.
- Fig. 6. Polyp of same showing spicular tracts.
- Fig. 7. Villogorgia compressa, n. sp. Spicules (a) of the operculum, (b) of the coenenchyma, (c) of the polyp.
  - Fig. 8. Chrysogorgia constricta, n. sp. A branch. × 2.
  - Fig. 9. Same. Two terminal polyps. ×12.
  - At the base is a young polyp not yet fully developed.
  - Fig. 10. Same. Spicules.
  - Fig. 11. Primnoisis ambigua. Spicules.
  - Fig. 12. Keroeides gracilis. Portion of branch showing arrangement of spicules.
  - Fig. 13. Same. Spicules of the coenenchyma.
  - Fig. 14. Same. Part of the sclerogorgic axis.
  - Fig. 15. Keroeides pallida, n. sp. The end of a branch showing arrangement of spicules.
  - Fig. 16. Same. Spicules (a) of the coenenchyma, (b) of the polyp.

#### PLATE XXIII.

- Fig. 1. Verrucella guadalupensis. Part of the Colony. ×21.
- Fig. 2. Verrucella guadalupensis. A branch, × 4, showing the manner in which the branches give support to the anemones, Peronanthus verrucellae, n. gen. et sp.



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## ZOOLOGICAL RESULTS

BASED ON MATERIAL COLLECTED IN

NEW BRITAIN, NEW GUINEA, LOYALTY ISLANDS

AND ELSEWHERE.

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# ZOOLOGICAL RESULTS

BASED ON MATERIAL FROM

# NEW BRITAIN, NEW GUINEA, LOYALTY ISLANDS AND ELSEWHERE,

COLLECTED

DURING THE YEARS 1895, 1896 AND 1897,

BY

ARTHUR WILLEY, D.Sc. Lond., Hon. M.A. Cantab.

LATE BALFOUR STUDENT OF THE UNIVERSITY OF CAMBRIDGE.

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# ORTHOGENETIC VARIATION IN THE SHELLS OF CHELONIA'.

## By HANS GADOW, M.A., Ph.D., F.R.S.,

University Lecturer in the Advanced Morphology of Vertebrates and Strickland Curator in the University of Cambridge.

#### With Plates XXIV—XXV.

DR WILLEY has handed over to me 20 new-born specimens of *Thalassochelys caretta*, the Loggerhead, collected by him from one nest in New Britain or Neu-Pommern. He preserved them after noticing that they exhibited great variations, in so far that none of them had the normal number of scutes.

I have supplemented this material by examination of the specimens in the British Museum of Natural History, and I am indebted to Dr Van Lidth de Jeude and to Dr Oudemans for photographs and descriptions of others in the Leiden Museum, and in the collection of the Royal Zoological Society "Natura Artis Magistra" at Amsterdam. I am now acquainted with no less than 76 specimens, ranging from the new-born to the adult.

Mr G. A. Boulenger, F.R.S., has also kindly helped me with valuable additional material and advice.

It is a well-known fact, at least to herpetologists, that this species of Turtle frequently possesses one or more "supernumerary scutes" and a critical study of these variations has led to what I take to be an explanation of their meaning.

In the following list of the specimens examined "size" is expressed by the length of the carapace in inches. The number of marginals is 13 on either side, unless noted differently.

B.M. means that the specimen is in the British Museum.

For simplicity's sake all the median epidermal scutes are mentioned as neurals, including the first or so-called nuchal.

<sup>&</sup>lt;sup>1</sup> A condensed account of this investigation was read, supplemented by diagrams, at a Meeting of the Cambridge Philosophical Society on Monday, November 14th, 1898.

| her           |            |  | N       | amber<br>scute: |               |  |         |
|---------------|------------|--|---------|-----------------|---------------|--|---------|
| Serial Number | Size       | Locality                                     | Neurals | Left costals    | hight costuls | Observations   | Figures |
| 1             | New born   | B. M. Karachi                                | 8       | x               | s             | Complete reduction of the three triangular vestigial costal scutes would turn this specimen into 8, 6, 7 with the 4th right costal as small as in many other specimens. It would then resemble specimen No. 5.  Reduction of the 5th and 7th neurals would produce 6, 6, 6, a very common condition.   | 1       |
| 2             | 2 feet     | B. M. Museat                                 | 8       | ī               | 7             | Both sides quite symmetrical. 7th neural very small.   | 2       |
| 3a            | New born   | B. M. Indian<br>Seas. Theobald<br>Collection | 8       | 1               | 7             | 7th neural very small. Right 4th costal small.   | 3       |
| 3b            | New born   | Leiden Museum                                | 8       | 7               | 7             | 5th neural and both 4th costals small.   |         |
| <b>3</b> c    | New born   | Leiden Museum                                | 8       | 7               | 7             | 5th neural, 4th right and both 7th costals small.  |         |
| 4             | New born   | B. M. Karachi                                | 8       | 6               | 7             |  | 4       |
| 5             | New born   | B. M. Borneo.<br>Bleeker Collect.            | 8       | 6               | -             | 5th neural almost suppressed; right 4th costal small. Cf. No. 1.   | 5       |
| 6             | Full grown | Cambridge Mus.                               | 8       | 6               | 6             | 1st, 5th, 6th and 7th neurals very small.  |         |
| 7.4           | New born   | B. M. Karachi                                | *       | 5               | f             | A very rare condition. Fusion of the most anterior pair of scutes would turn this specimen into 8, 5, 6; and the last but one, very small, neural would then be the 7th scute, as is the case in numbers 1, 2, 3, 17. Further suppression of the little triangular anterior neural and of the last but one neural would turn this specimen into 6, 5, 6, an otherwise unknown condition, but resembling No. 39, its twinspecimen, provided in the latter the two anterior scutes become fused. | 6       |
| 77            | New born   | ${ m Amsterdam}$                             | `       | õ               | б             | 5th and 7th neurals very small. 5th and 6th right costals small.   |         |
| 8             | New born   | New Britain.<br>Willey, 1                    | 7       | 7               | 7             |  | 7       |
| 9             | New born   | Willey, 2                                    | 7       | 7               | 7             | 4th right costal and 5th neural small.   | 8       |
| 10            | New born   | Willey, 3                                    | ī       | 7               | -             | 4th left costal small. 5th neural extremely small.   | 9       |
| 11            | New born   | Willey, 4                                    | 7       | -               | 7             | 5th neural small. 4th right and left costals reduced to triangular distally placed scutes.   | 10      |

|               |           |   |         |                 |               |  | _       |
|---------------|-----------|---|---------|-----------------|---------------|--|---------|
| lber          |           |   |         | amber<br>scute: |               |  | 70      |
| Serial Number | Size      | Locality  | Neurals | Left costals    | Right costals | Observations   | Figures |
| 12            | New born  | B. M. Manado                                      | 7       | 7               | 7             | 5th neural very small. 4th right and left costals much reduced.  |         |
| 13            | New born  | B. M. Batavia.<br>Bleeker Collect.                | 7       | <u>t</u>        | 7             | 6th neural very small. This would be very exceptional, but the same scute is also the last but one, and this coupled with the small size of the right and left 4th costals, while the 5th neural is large and not small as is usual in such cases) suggests that in this specimen the original 5th neural has already fallen out.                        | 1       |
| 14            | New born  | Willey, 5   | ī       | -               | 6             | There are 14 marginals on the left side and the lateral corner is formed by the 6th. This supernumerary condition is caused by the two first marginals being very small and not yet being fused into one larger scute as on the right side, which is normal. Cf. specimen No. 15d.   | 12      |
| 150           | New born  | Willey, 6   | 7       | -               | 6             | 7th left costal small.   | 13      |
| 15b           | New born  | Leiden Museum                                     | 7       | 7               | 63            | 5th neural and 4th left costal small.  |         |
| 16            | New born  | B. M. Indian<br>Seas. Theobald                    | 7       | 7               | 65            | 5th neural and 4th left costal small.  |         |
| 170 ;         | New born  | B. M. Indian<br>Seas. Theobald                    | 4       | G               | 6             | Last but one neural and 6th right costal very small. There are apparently only 7 neurals, but the first neural is very large and shows by its composite shape that it has been produced by fusion of two successive neurals; cf. specimen No. 24. Counting this large neural scute as 1+2, the last but one would be the 7th as in specimens 1, 2, 3, 7. | 14      |
| 17/           | New born  | Manchester Mus.                                   | -       | 5               | 6             | (Added during correction of proof.)  |         |
| 18a           | 8 inches  | B. M. Muscat                                      | 7       | 5               | 5             | 2nd neural extremely small and asymmetrical. 13 right and 14 left marginals, and the 6th left forms the lateral corner as in specimen No. 14.  | 15      |
| 15/           | 8 inches  | Amsterdam   | -       | 5               | 5             | 5th neural small. 12 right and 13 left marginals.  |         |
| 190           | New born  | B. M. Little<br>Cayman, Lieut,<br>Carpenter Coll. | 7       | 5               | 5             | None of the neurals are reduced. The specimen is quite symmetrical. There are only 12 marginals on either side, and the lateral corner is formed by the 4th marginals.   | 16      |
| 195           | 13 inches | Amsterdam   | 7       | 5               | 4             | 6th (last but one) neural very small, the 1st left costal very small, the corresponding right scute being absent. See remarks on stage VII. p. 218.  | 26      |
|               |           |   |         |                 |               | 20 2   | 1       |

| ıber          |          |   |         | mbe          |               |  |         |
|---------------|----------|---|---------|--------------|---------------|--|---------|
| Serial Number | Size     | Locality                                | Neurals | Left costals | Right costals | Observations   | Figures |
| 20            | New born | Willey, 7                               | 6       | 7            | 7             | Right 4th costal much reduced  | 17      |
| 21            | New born | Willey, 8                               | 6       | 7            | 7             | Left 4th costal small  | 18      |
| 22            | New born | Willey, 9                               | 6       | 7            | 6             | Left 4th costal small. Only 12 marginals on the right side.  | 19      |
| 23            | New born | Willey, 10                              | 6       | 7            | 7             | Left 4th costal small. Only 12 marginals on either side; the lateral corner is formed by the 4th. The first marginal is unusually long, indicating previous fusion of two.   |         |
| 24            | 4 inches | B. M. Philippines                       | 6       | , 6          | 7             | 5th neural very small. 4th and 5th right costals small. This specimen seems to have only 6 neurals, but in reality the 1st neural is composed of two successive scutes as indicated by its size and shape. Moreover the small size of the 4th right costal scute indicates that the corresponding neural (between the present 3rd and 4th) has fallen out. The specimen can therefore be reconstructed into 8, 7, 7, and the last but one neural (the present 5th) would be the original 7th. This specimen bears great resemblance to No. 17. |         |
| 25            | New born | B. M. Mazatlan                          | 6       | 7            | 1 6           | 4th left costal small.   |         |
| 26            | New born | Willey, 11                              | 6       | 6            | 7             | Right 4th costal small.  |         |
| 27            | New born | Willey, 12                              | 6       | 6            | 7             | Right 4th costal small. 13 right marginals, corner formed by the 5th; 14 left marginals, corner formed by the 6th.   | 21      |
| 28            | New born | Willey, 13                              | 6       | 6            | 6             | 1st and 2nd neurals partly fused with each other.  | 22      |
| 29            | New born | Willey, 14                              | 6       | 6            | 6             | 14 marginals on either side, the 1st marginal scutes being very small.   |         |
| 30            | New born | Willey, 15                              | 6       | б            | 6             | •  |         |
| 31            | New born | Willey, 16                              | 6       | 6            | 6             |  |         |
| 32            | New born | Willey, 17                              | 6       | 6            | 6             |  |         |
| 33            | New born | Willey, 18                              | 6       | 6            | 6             |  |         |
| 34            | New born | Willey, 19                              | 6       | 6            | 6             |  |         |
| 35            | New born | Willey, 20                              | 6       | 6            | б             | 13 left, 12 right marginals  | 23      |
| 36            | New born | B. M. Indian<br>Seas, Theobald<br>Coll. | 6       | 6            | 6             |  |         |

| ıber          |            |   |         | scute:       |               |  |         |
|---------------|------------|---|---------|--------------|---------------|--|---------|
| Serial Number | Size       | Locality                                | Neurals | Left costals | Right costals | Observations   | Figures |
| 37            | New born   | B. M. Indian<br>Seas. Theobald<br>Coll. | б       | 6            | 6             |  |         |
| 38            | New born   | B. M. Indian<br>Seas. Theobald<br>Coll. | 6       | 6            | 6             |  |         |
| 39            | New born   | B. M. Mazatlan.<br>Forrer Coll.         | 6       | 6            | 6             |  |         |
| 40            | New born   | B. M. Manado                            | 6       | 6            | 6             |  |         |
| 41            | New born   | B. M. Manado                            | 6       | 6            | 6             |  |         |
| 42            | New born   | B. M. Karachi                           | 6       | 6            | 6             |  |         |
|               | New born   | B. M. Karachi                           | 6       | 6            | 5             | This specimen resembles No. 7 in so far as the neural series begins with a double scute. By fusion of this anterior pair of scutes the specimen would turn into 6, 6, 5 and then begin to resemble specimen No. 7. Suppression of the left 5th costal scute would further change this specimen into the normal condition of 6, 5, 5.  On the other hand, if the anterior pair of scutes were looked upon as costals, this specimen would be absolutely abnormal, as it would in this case have only 5 median scutes. | 24      |
| 44            | 15 inches  | В. М.                                   | 6       | 6            | 5             | A small triangular scute remains intercalated between the 1st and 3rd costal on the left side.   | 25      |
| 45            | New born   | B. M. Little<br>Cayman                  | 6       | 5            | 5             | Quite normal except that there are only 12 marginals on either side, the 4th forming the lateral corner.   |         |
| 46            | New born   | B. M. Australia.<br>Shark's Bay         | 6       | ð            | 5             | Quite normal except that there are only 12 marginals on either side, the 4th forming the lateral corner.   |         |
| 47            | New born   | B. M. Australia.<br>Shark's Bay         | 6       | 5            | ð             | Quite normal except that there are only 12 marginals on either side, the 4th forming the lateral corner.   |         |
| 48            | 3 inches   | В. М.                                   | 6       | 5            | 5             | Quite normal.  |         |
| 49            | 3.7 inches | Amsterdam                               | 6       | 5            | 5             | Quite normal.  |         |
| 50            | 8 inches   | Leiden Museum                           | 6       | 5            | 5             | Normal.  |         |
| 51            | 8 inches   | Leiden Museum                           | 6       | 5            | 5             | Normal.  |         |
| 52            | 8 inches   | Leiden Museum                           | 6       | 5            | 5             | Normal.  |         |

| iber          |               |                            |         | mber<br>scutes |               |  |
|---------------|---------------|----------------------------|---------|----------------|---------------|--|
| Serial Number | Size Locality |                            | Neurals | Left costals   | Right costals | Observations   |
| 53            | 8 inches      | Leiden Museum              | 6       | 5              | 5             | Normal.  |
| 54            | 12 inches     | В. М.                      | 6       | 5              | 5             | Quite normal except that there are only 12 right marginals, the 4th of which forms the lateral corner. |
| 55            | 14 inches     | Amsterdam                  | 6       | 5              | 5             | Normal; 12 marginals on either side.   |
| 56            | 14 inches     | B. M. Atlantic             | 6       | 5              | 5             | Normal, except marginals which are like those of the previous specimen.                                |
| 57            | 14 inches     | B. M. Atlantic             | 6       | 5              | .5            | Quite normal.  |
| 58            | 14 inches     | B. M. Atlantic             | 6       | 5              | 5             | Normal. Only 12 marginals on either side.  |
| 59            | 18 inches     | В. М.                      | 6       | 5              | 5             | Normal. Only 12 marginals on either side.  |
| 60            | 18 inches     | Leiden Museum<br>Sardinia  | 6       | 5              | 5             | Normal.  |
| 61            | 18 inches     | Leiden Museum<br>Surinam   | 6       | 5              | 5             | Normal.  |
| 62            | 18 inches     | Mus. Van Lidth<br>de Jeude | 6       | 5              | 5             | Normal.  |
| 63            | 25 inches     | Leiden Museum<br>Livorno   | 6       | 5              | 5             | Normal.  |
| 64            | Full grown    | Leiden Museum<br>Livorno   | 6       | 5              | 5             | Normal.  |
| 65            | Full grown    | В. М.                      | 6       | 5              | 5             | Normal.  |
| 66            | Full grown    | В. М.                      | 6       | 5              | 5             | Normal.  |
| 67            | Full grown    | В. М.                      | 6       | 5              | 5             | Normal.  |
| 68            | Full grown    | В. М.                      | 6       | 5              | 5             | Normal.  |
| 69            | Full grown    | Holland,<br>Leiden Museum  | 6       | 5              | 5             | Normal.  |

The following table contains the variations or combinations in the number of scutes which can possibly occur. Those which have actually been observed are indicated by black type. The whole number of possibilities amounts to 30, and it seems only a question of greater material than has been at my disposal to find the hitherto missing variations. From the morphological point of view it is of course immaterial if the right or the left side contains the greater number of costals.

| Neurals. | Costals.        | Neurals. | Costals.  | Neurals. | Costals.        |
|----------|-----------------|----------|---|----------|-----------------|
| 8        | 8.8             | 7        | 8.8   | 6        | 8.8)            |
|          | 8.7             |          | 8.7   |          | 8.7 very        |
|          | 8.6             |          | 5.61  |          | 8.6 improbable. |
|          | 8.5 improbable. |          | $\left\{\begin{array}{c} 8.5 \\ 8.5 \end{array}\right\}$ improbable | •        | 8:5             |
| 8        | 7.7             | 7        | 7.7   | 6        | 7.7             |
|          | 7.6             |          | 7.6   |          | 7.6             |
|          | 7:5             |          | 7:5   |          | 7.5             |
| 8        | 6.6             | 7        | 6.6   | 6        | 6.6             |
|          | 6.5             |          | 6.5   |          | 6.5             |
|          | 5.5             |          | 5.5   |          | 5.2             |

The chief abnormalities are distributed as follows.

With eight neural scutes: eight new-born, and two adults.

With seven neural scutes: 13 new-born, one of 13, and two of 8 inches.

With six neural scutes, but with abnormal costals: 23 new-born and two young (of 4 and 8 inches).

Of these 51 abnormal specimens 26 are serious in so far as they refer to specimens with seven or eight neural scutes, while only two of these specimens (numbers 18 and 19) have normal costals. Moreover of these 26, only five are not baby specimens.

Of the remaining 25 abnormal specimens only two are not babies. Not less than 15 of them are quite symmetrical with the formula 6, 6, 6; 4 are asymmetrical by possessing one extra right and two extra left costal scutes or vice versa, and four are symmetrical, possessing seven instead of five pairs of costal scutes.

In every case in which the last but one median scute is very small or vestigial it is the 7th scute; in other words the last but one neural occurs in a vestigial condition only in specimens with the large number of eight neurals. This applies even to the two specimens Nos. 13 and 17 in which there are now only seven neurals, but which by deduction can be shown to have possessed the original full number of eight neurals. Moreover in none of those specimens with a vestigial last but one neural (Nos. 1, 2, 3, 7, 13, 17, 19b) are any of the corresponding 6th or 7th pairs of costals exceptionally small. It seems reasonable to suppose that, whilst the last but one neural dwindles away, the last pair of costal scutes increases in size. An indication of this process is the frequently crowded position of the proximal ends of the two last pairs of costal scutes.

In a considerable number of specimens (17 new-born specimens and one 4 inches long) the 4th costal scute is abnormally small, and this reduction coincides in eight cases with a half-suppressed condition of the 5th neural. It is significant that seven of the specimens with such a reduced 5th neural still possess either eight or seven neurals,

while in almost every one of those specimens with six neurals and reduced 4th costals no corresponding reduction in the size of the neurals is visible. The only exception

| Chelonians arranged according to the number of neural and costal scutes                            | Neural | Costal | Total |
|--|--------|--------|-------|
| 1  | . 8    | 16     | 24    |
|  | 8      | 14     | 22    |
|  | 8      | 13     | 21    |
|  | 8      | 12     | 20    |
|  | 8      | 11     | 19    |
|  | 7      | 14     | 21    |
| 1  | 7      | 13     | 20    |
| Thalassochelys caretta as observed   | 7      | 12     | 19    |
|  | 7      | 11     | 18    |
|  | 7      | 10     | 17    |
|  | 7      | 9      | 16    |
|  | 6      | 14     | 20    |
|  | б      | 13     | 19    |
|  | 6      | 12     | 18    |
|  | 6      | 11     | 17    |
| This is the normal number for <i>Th. caretta</i> and also the Highest Normal number among Chelonia | 6      | 10     | 16    |
| Chelone imbricata and Chelone mydas, Testudo and the majority of Tortoises                         | . 6    | 8      | 14    |
| Many Pleuroderous Tortoises and certain species of Testudo (lowest normal number                   | 5      | 8      | 13    |

is specimen No. 24 (a 4 inch shell) which, as explained on p. 210, is abnormal in several respects. The obvious way of accounting for this want of correspondence between reduced 4th costals and an apparent reduction of a neural is that in these specimens the original 5th neural has already been completely suppressed, anyhow that it is wanting. Reduction of the last but one neural reduces a specimen from eight to seven neurals, and reduction of the original 5th reduces such a shell to one with six neurals only. In a similar way the number of eight or seven costals is reduced to six by suppression of the 4th pair of costals.

Let us now examine those Turtles which possess the normal number of six neurals but still with six pairs of costals instead of the final number of five costals. There are not less than 15 such specimens, all new-born. In some of them, for instance,

numbers 16 (Willey 11) and 28 (Willey 13), the 5th pair is somewhat smaller than the rest. A reduction in size is likewise present in the 5th costal where this happens to be the last but one, as in No. 12 (left side), No. 43 (left side); and especially in this last specimen it is very obvious how the costals are reduced from six to five in number by the last but one (or 5th pair) disappearing. Moreover a disturbance in this region is indicated by the shape of the last but one neural in so far as this scute has often eight or seven sides instead of its regular hexagonal shape, e.g. numbers 8, 9, 10, 14, 21, 22, 23, 26, 27, 43.

Especially instructive are those asymmetrical specimens with six neurals and with the five normal costal scutes on one side but still with six costals on the other side<sup>1</sup>.

The marginal bones shew very little variation. The normal number consists of 13 pairs, the 5th of which forms the lateral angle of the carapace. Occasionally there are as many as 14 marginals, and in these cases the angle is invariably formed by the 6th; or there are only 12, and there the 4th forms the angle. This shews that the reduction from 14 to 13 or to 12 is caused by the fusion of two neighbouring marginals into one. In several new-born specimens such a fusion is still incomplete.

We know that almost all recent Tortoises and Turtles possess 10 pairs of ribs, but 10 to 12 median dermal bones, eight of which are attached to, or fused with the spinous processes of as many vertebrae, while one dermal bone, in front—the so-called nuchal,—and one to three bones behind—the so-called pygal plates, are no longer in connexion with a vertebra.

Moreover it is reasonable to assume that originally each complete metamere or segment in the region of the trunk proper had a vertebra, one pair of ribs, one neural and a pair of costal dermal plates. Certain fossil Chelonians shew this arrangement, or something approaching it.

The suggestion is obvious that to each complete metamere belonged also a complete set of epidermal scutes, namely, one median and a pair of lateral or costal scutes, something like the arrangement of the armour in Crocodiles and allied fossil Reptiles.

It is therefore reasonable to assume that a greater number of successive transverse series of neural and costal scutes represents a phylogenetically older, more primitive, or atavistic stage.

It is almost certain that the alternating or interlocking position of the costals and neurals is a secondarily acquired feature. Just as the regular hexagonal shape of the neurals is not a primitive but a neat and comparatively late arrangement. This consideration applies equally to the epidermal scutes and to the underlying dermal, neural and costal bony plates. It is well known that the epidermal scutes and the dermal plates do not at all correspond with each other, but scarcely any attention has been drawn to the important fact that the relative position of these various elements changes considerably during the growth of the individual creature;

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<sup>&</sup>lt;sup>1</sup> Of course it is quite conceivable that reduction from 6 to 5 costals can be brought about in another way. Specimen No. 44 affords such an instance by the vestigial second left costal, but I have at last come to the conclusion that this little scute should be homologised with the 2nd scute of specimen No. 1 as a very old and therefore rare survival.

some scutes and plates increase steadily in size, while others remain comparatively stationary, so that in the latter case they apparently undergo a reduction or even suppression.

Let us now arrange the various Chelonians, first *Thalassochelys caretta*, according to the hints which we have received from the analytical examination of the specimens

catalogued above.

- Stage I. Hypothetical. Eight neural and eight pairs of costal scutes. Neurals and costals to lie in the same transverse plane.
- Stage II. Eight neurals and eight pairs of costals, the latter fitting with their median or proximal ends in between two successive costals. This rearrangement seems to have been brought about by the partial reduction of one pair of costal scutes. This reduced scute is probably the 2nd costal. Cf. nos. 1 and 44.
- Stage III. Eight neurals and seven pairs of costals. The original 2nd costal having been suppressed, the original 3rd has now become the actual 2nd and abuts between the second and third neural, the rest following correspondingly: the actual 4th (the original 5th) now lying between the 4th and 5th neural, *i.e.* half in front of the latter to which it genetically belongs, as is still indicated by its evident sympathy with this neural.—Nos. 2 and 3. (Text fig. III<sup>a</sup> and III<sup>b</sup>.)
- Stage IV. Seven neurals and seven pairs of costals. Brought about by reduction of the original 7th or last but one neural, the last neural has thereby become the actual 7th in nos. 8—13, while nos. 2 and 3 represent an intermediate stage in the condition of the 7th neural.
- Stage V. Seven neurals and seven pairs of costals, but the 5th neural and the 4th pair of costals are in a state of reduction. Cf. nos. 9, 10, 11, 12.
- Stage VI. Six neurals and six pairs of costals, owing to complete suppression of the 5th neural and the 7th pair of costals. The original 6th neural is now number 5 and the last is now number 6, late 7, late 8. A similar rearrangement of the serial numbering applies to the costals; the 3rd (late 4th of stage I.) and the late 5th having now become neighbours. Cf. nos. 28—42 with numerous instances intermediate between the last two stages. (Text fig. VI<sup>a</sup> and VI<sup>b</sup>.)

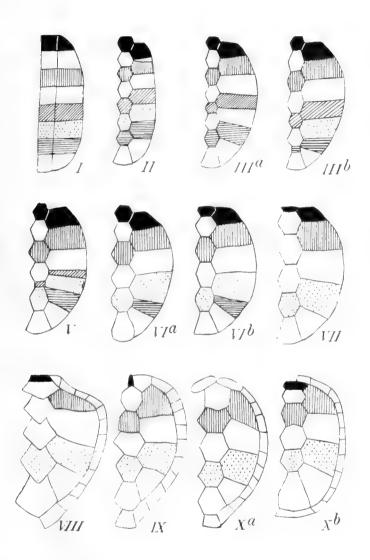
<sup>1</sup> This change in the numbering of the scutes shows how difficult it is to arrive at the true homologies of the individual parts which exhibit meristic variation. It will often be absolutely impossible to homologise such parts unless we know the whole developmental history of the whole creature, or as in the present case, unless we can study an ample material which provides almost every theoretically possible intermediate stage, or which comprises certain individual variations which can be submitted to a crucial test. Arguing by deduction we can then (e.g. specimens, numbers 7, 13, 17, 24, 43) check the correctness of the conclusions which we have arrived at by the inductive method.

In Thalassochelys the numerical changes are as follows:

Starting with 8 neurals, suppression of the 7th neural turns the original 8th, or last, into the actual 7th, subsequent suppression of the 5th turns the original 6th into the 5th and the 7th, late 8th, into the 6th neural. Ultimate loss of the 1st, e.g. in Testudo sumeirei changes the 2nd into the now actual 1st and the last of all, the late 8th, late 7th, late 6th into the 5th.

 $\Delta$  similar rearrangement of numbers is necessary with the costals after the dropping out of the original 2nd, the 5th and one or two of the last pairs.

In order to avoid confusion as much as possible, the true homologies of the scutes have been indicated in the diagrams (p. 217) by corresponding shading.



Diagrams to illustrate the progressive reduction of the epidermal scutes in various Chelonians. The Roman numerals denote the stages enumerated on pages 216 and 218. The scutes whose fate it is desired to follow are indicated by distinctive shading.

Stage VII. Six neurals and five pairs of costals owing to fusion of the two last pairs of costals into one, or perhaps by suppression of one pair as indicated by numbers 26 and 28. This is the normal condition of Thalassochelys, and further reduction of scutes in this species was unknown until Dr Oudemans sent me a drawing of specimen No. 19b (Fig. 26), which but for the vestigial last but one neural would be intermediate between stages VII and VIII.

But in other Genera and families the reduction goes much further, leading to the following stages.

Stage VIII. Six neurals and only four pairs of costal scutes. This condition is typical of the two species of the genus *Chelone*, *Ch. mydas* and *Ch. imbricata*. Now behold, the costal scutes fit everywhere into the corners which are formed by two successive median scutes, except between the first and second, which here for the first time come together without any interference of a pair of costals. This condition results from the suppression of the first pair of costals in comparison with other Turtles. It is however a remarkable fact that hitherto no atavistic variations in the young of *Chelone imbricata* have been observed. This species seems to be, so far as the development of its dorsal scutes is concerned, quite cenogenetic<sup>1</sup>.

Stage IX. Six neurals and only four pairs of costal scutes, but the first median scute, the so-called neural, has become very small, the resulting gap being filled up by an enlargement of the first pair of marginals. Observe also in *Testudo*, e.g. T. mauritanica, the lateral angles of the second median scute, which frequently are still persistent, although there is no longer a pair of costal scutes to fit into. This stage or condition is the normal one in most cryptoderous tortoises. Supernumerary scutes occur occasionally, for instance, in *Testudo* and *Chrysemys*.

Stage X. The nuchal shield has disappeared, and there is either left a little gap, or this is closed by the first pair of marginals (X<sup>a</sup>). The whole carapace is composed of five neural and four pairs of costal scutes, in all only 13 scutes, omitting of course the marginals. This condition occurs specifically and even individually in the Genus Testudo. It is normal also in pleuroderous tortoises, but in some of these, for instance in Sternothaerus, the number of five separate median scutes seems to be due not to suppression but to fusion of the original first or nuchal with the next following scute (X<sup>b</sup>). Consequently this condition would represent a side departure or separate stage, somewhat intermediate between the VIIIth and last stage.

Beyond this Xth stage Chelonians have not yet ventured, at least not normally<sup>2</sup> and it is not our business to enquire what they perhaps may do in the future, but we can, by the help of comparative anatomy, reconstruct to a certain extent, the ancestral type.

<sup>&</sup>lt;sup>1</sup> "Supernumerary" scutes seem to be very rare in the genus Chelone. I did not know of a single abnormal specimen until Dr Willey found one of Ch. mydas (in the Manchester Museum) with 7 neurals, 5 left and 4 right costals.

<sup>&</sup>lt;sup>2</sup> The greatest, although quite abnormal, reduction I am acquainted with occurs in a specimen of the now extinct Testudo indica (figured by Perrault, Mém. pour servir à l'histoire des animaux et des plantes, Amsterdam, 1736; cf. also Gadow, "On the remains of gigantic Land-Tortoises, and of an extinct Lizard, recently discovered in Mauritius," Transact. Zool. Soc. XIII. pt. VIII. 1894). This specimen has no nuchal and only 4 other median or neural scutes.

There can be no doubt of the former existence of Chelonians which normally possessed eight median and eight pairs of costal epidermal scutes, and that these corresponded with the usual number of eight transverse series of dermal bony plates. As many as 11 median dermal bones are known in some fossil forms with as many as 10 pairs of costal plates, corresponding with 10 rib-bearing dorsal vertebrae. In Chelydra serpentina there are not less than 12 median plates, including the last unpaired "marginal."

A reduction from plated to free, unarmoured dorsal vertebrae has taken place, and does still take place, at the root of the neck, and behind the sacrum at the root of the tail. Since there are from 11 to 12 to 13 to 14 pairs of marginal scutes, it is reasonable to assume 14 as the highest indicated number of metameres which have entered into the composition of the dorsal shell. Those early tortoises must have been more elongated and far less broad than any known Chelonian.

Moreover, the recent Macroclemmys temmincki possesses three to four so-called supramarginal scutes (analogous to the inframarginals of Chelydridae and Dermatemydidae) which indicate the original typical number of longitudinal scutes, seven in all, on the back, namely, an unpaired median, a pair of costal, a pair of supramarginal, and a pair of marginal elements. There can also be little doubt but that the median series was originally double or paired; cf. specimens, numbers 7 and 43, and the analogy with Crocodiles.

The so-called first pair of marginal plates of Dermatemydidae and Cinosternidae has underlying a pair of rib-like processes, and the fossil *Chelydropsis* has two successive "nuchal plates."

All recent Chelonians possess eight free cervical vertebrae and ten dorsal vertebrae, including the sacrals, but the fusion of the vertebrae and ribs with the carapace is restricted to eight vertebrae and ribs, the 1st dorsal (9th of the whole series) and the 10th dorsal (18th of the whole series) possessing each only a very thin and small pair of ribs which do not enter into the formation of the carapace by fusion with a pair of costal plates.

Then follow several, from one to three median dermal plates, the so-called pygal plates, without corresponding lateral or costal plates. The first pygal belongs to the last dorsal or 18th vertebra. The last pygal cannot be distinguished from a pair of fused marginals.

This is the arrangement of the majority of Chelonians, but in the Genera Cistudo, Cinosternum, Dermatemys and Staurotypus the actual connexion of the carapace with the vertebral column is now restricted to the 10th to 14th vertebrae.

I therefore conclude that at an early ancestral stage, not necessarily that of the primordial Chelonian, the plates and scutes of the back were arranged as follows:

All the metameres carried originally a series of transversely arranged dermal plates and scutes, which in the region of the trunk, according to the greater bulk of the body, increased in size, converging towards the root of the neck and upon the tail.

About 14 metameres were distinguished by the greater size of the dermal plates, each transverse series consisting of a median or neural and three pairs of lateral elements, in all eight. The median pair fused into an unpaired neural. The next

lateral pair became the costal, the outermost or most lateral the marginal set. The intermediate row between these two still survives in some recent genera as the so-called supramarginals; it became gradually suppressed owing to the increasing size of the costals.

The last costals, say those of the 18th to 20th metameres, became likewise suppressed, in conformity with the shaping of the trunk; the three last neurals were turned into pygals and the last pair of marginals closed round the posterior end, meeting in the middle line, and there they occasionally fuse, for instance in *T. mauritanica*, into an unpaired plate which is covered by a likewise unpaired epidermal scute.

A similar reduction seems to have taken place at the root of the neck. The first of the original 14 marginals is, in *Dermatemys* and in *Cinosternum*, still in a debateable condition. It may be a pair of true marginals, or it may represent the pair of costals of the 8th vertebra provided the corresponding neural element has fallen out. At least it seems to explain how by an analogous process the median element of the 9th vertebra, the so-called nuchal, has been produced. Unfortunately, nothing is known as to what might be used as a criterion for determining the nature of these so-called first marginals. The study of the ontogenetic history of *Dermatemys*, or of *Cinosternum*, will probably solve this question.

A later phylogenetic stage would be characterised by the suppression of the supramarginals, and by the reduction from eight to seven to six and ultimately to even

THE FREQUENCY OF THE ABNORMALITIES.

| Length of<br>carapace<br>in inches | Number of<br>abnormal<br>specimens | Number of<br>normal<br>specimens | Percentage of abnormal specimens  |
|------------------------------------|------------------------------------|----------------------------------|---|
| New born                           | 44                                 | 3                                | Of the 47 new-born specimens not less than $93.6^{\circ}/_{o}$              |
| 3 inches                           | _                                  | 1                                |   |
| 3.7 inches                         | -                                  | 1                                | Of the 9 specimens from 3 to 8 inches: $33^{0}/_{0}$                        |
| 4 inches                           | 1                                  | _                                |   |
| 8 inches                           | 2                                  | 4                                | Of the 19 specimens from 8 to 24 inches: $26{}^0/_0$                        |
| 12 inches                          | _                                  | 1                                | Of the 7 large specimens only $14^{0}_{/0}$                                 |
| 13 inches                          | 1                                  | _                                |   |
| 14 inches                          | _                                  | 4                                |   |
| 18 inches                          | 1                                  | 4                                |   |
| 24 inches                          | 1                                  | 1                                |   |
| Large                              | 1                                  | 6                                |   |
|                                    | 51                                 | 25                               | Of the total of 76 specimens $66^{0}/_{\scriptscriptstyle 0}$ are abnormal. |

less transverse series of epidermal scutes, while the constituting elements of the dermal armour after having been welded into the formation of the carapace, remain comparatively constant.

But to return to Thalassochelys caretta.

This table shews that the abnormalities are 4 to 7 times as common in the newborn as in the mature specimens, and that their frequency decreases from the smaller to the larger and very large specimens.

We have no business whatever to assume that our little Turtlets which are born with irregular scutes are therefore doomed to perdition, while only those born with the normal number are predestined to live and to propagate the race. Such an assumption is at once contradicted by the fact that no less than  $14\,^\circ$ / $_{\circ}$  of large turtles are wrong in their scutes, and do, or did very well, for all we know to the contrary.

Of course comparatively very few individuals of a brood of several dozen Turtlets reach maturity, but they meet with their death through Sea-birds, Crocodiles, Sharks, and similar enemies, which in all probability swallow them regardless of the number and disposition of their victims' scutes.

These abnormalities are atavistic reminiscences, and most of the creatures grow out of these irregularities by the reduction or squeezing out of certain of the scutes. Why this suppression should take place in the region of the original 7th and 5th transverse series of neural and costal scutes I do not profess to know.

We have here an instance of a widespread evolutionary law, namely, that the number of a serial set of organs or parts has a tendency towards reduction in numbers, while the remaining parts are better developed, are more neatly finished and can therefore be made more highly effective.

The eight or nine gill-supporting visceral arches of the early Elasmobranchi are reduced to five or four or even less gill-bearing arches in the Teleostomi with highly finished pectinated gills. The multiserial fish-fin has been changed into our pentadactyle limb. The innumerable skin-denticles, the shagreen of Elasmobranchs, have produced the dermal plates and bones of higher creatures. Of the six primitive arterial arches there remain only three, or may be two, etc., etc.

Our Turtlets start with many, with at least 24 dorsal scutes (leaving out the marginals), and they reduce them to 16. In other genera the reduction has advanced to 14, to 13, and individually even to 12.

This means onward development. The ideal, the goal for the young Caretta is the possession of a 16 scuted shell. Those which start with 24 perhaps never reach the ideal, but this failure does not seem to hurt them, natural selection remains indifferent. Others start with 22, 21, 20, 19 or 18 scutes, and the latter individuals are rather common in the newly hatched stage, and all of these seem to reach the goal. Lastly there are some precocious Turtlets of the same brood, which start with the right number of 16 scutes, but if they devote their superfluous energy to something better than the making of tortoise-shell we do not know.

Anyhow this is onward development. These variations from the normal type all lie in the direct line of descent, and the more serious the variation, the further back

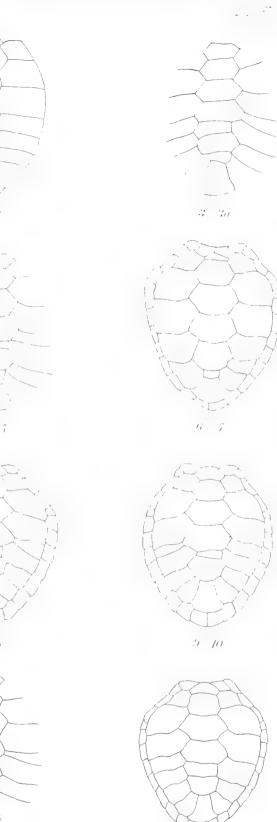
it points. Moreover the changes necessary to turn any given variation into another one less abnormal until ultimately the normal condition is reached, are not erratic but stand in strict correlation with each other and proceed strictly on definite lines. I therefore call this kind of atavistic variation orthogenetic.

Of course there is no proof of what I have tried to explain. Comparative anatomy and common sense tell us it is so. But common sense is not evidence in a sceptical court. The only way of proving the correctness of the view explained in this paper would be to take a number of abnormal turtlets and to watch, while they are growing up, if and how they mend their irregular shells and become normal.

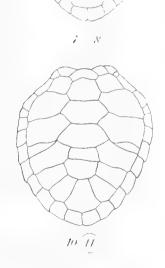
#### EXPLANATION OF PLATES XXIV. AND XXV.

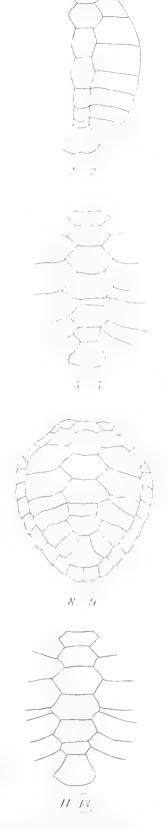
The numbers enclosed in circles correspond with the numbers of the specimens described in the list which commences on page 208. All the figures relate to young individuals of the marine Chelonian *Thalassochelys caretta*.

In the complete drawing reproduced in Fig. 18, Pl. XXV., attention may be drawn, apart from the scutes of the carapace, to the claws on the paddles and the unusually prominent tubercle in the nape of the neck. The figure is drawn to natural size.

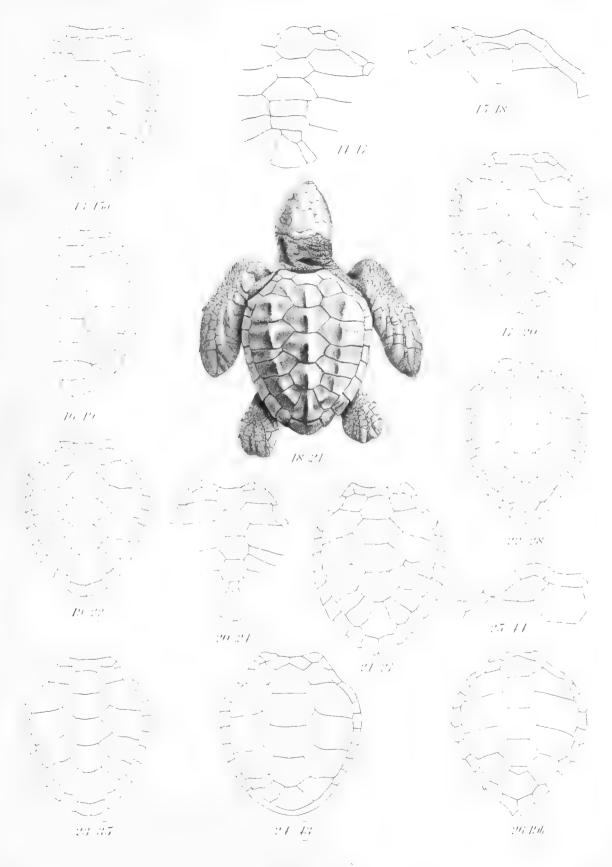


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# ENTEROPNEUSTA FROM THE SOUTH PACIFIC, WITH NOTES ON THE WEST INDIAN SPECIES.

## BY ARTHUR WILLEY, M.A., D.Sc.

[With Plates XXVI—XXXII.]

Nor more than five species of Enteropneusta have been described from the South Pacific up to the present time, and of these, no less than four have been definitely made known since the publication, in 1893, of Professor Spengel's Monograph of the group.

The five species are as follows:—Schizocardium peruvianum Spengel, Ptychodera australiensis Hill¹, Ptychodera flava Eschscholtz², Ptychodera hedleyi Hill³, and Spengelia porosa Willey.

In the present contribution I am able to add three new species to this list, namely, Spengelia alba n. sp., Ptychodera ruficollis n. sp., and Ptychodera carnosa n. sp. I also describe two new species of Ptychodera from the West Indies, specimens of which I owe to the kindness of Professor T. H. Morgan (see below p. 288).

Ptychodera flava was the first Enteropneust ever described, and was obtained from the Rumanzow Group in the Archipelago of the Marshall Islands, and described by Eschscholtz in 1825. The figure of the animal given by Eschscholtz was reproduced by Spengel in his monograph; and the general character of the species portrayed in this figure seemed to indicate that it was closely similar to the species which I found in great abundance at the Isle of Pines in 1896. But as Eschscholtz's figure did not admit of any detailed comparison with the form from the Isle of Pines, I deemed it advisable to give a provisional name to the latter, viz. Pt. caledonica.

I was subsequently informed by my friend Mr J. P. Hill that the same species occurs at Funafuti and I thereupon became doubtful as to the value of the name Pt. caledonica. Accordingly in a later publication I stated in a footnote that if the

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<sup>&</sup>lt;sup>1</sup> J. P. Hill (1894), "On a new species of Enteropneusta (*Ptychodera australiensis*) from the coast of New South Wales," *Proc. Linn. Soc. N. S. W.* x. (2).

<sup>&</sup>lt;sup>2</sup> A. Willey (1897), "On Ptychodera flava Eschscholtz," Q. J. M. S. Vol. xL. p. 165.

J. P. Hill (1898), "The Enteropneusta of Funafuti," Memoirs Aust. Mus. III. pp. 205 and 335.

<sup>4</sup> A. Willey (1898), "Spengelia, a new genus of Enteropneusta," Q. J. M. S. Vol. xL. p. 623.

species from the Marshall Islands should prove to be distinct, then its name (i.e. that given by Eschscholtz) would have to be changed. This, however, was a mistake on my part, since such a procedure would be contrary to the rules of priority in nomenclature. The present position of affairs with regard to this species is therefore, so far as I am concerned, the following. Until it is shown that the Northern and Southern species are different, Eschscholtz's name will apply to both. If, on the contrary, they should eventually prove to be distinct from one another, then the Southern species will be  $Pt.\ caledonica$  Willey and the Northern species alone  $Pt.\ flava$  Eschscholtz.

#### TERMINOLOGY.

Before proceeding further, I think it will be well to explain certain technical terms which it is necessary to introduce when treating of the Enteropneusta in one's mother-tongue. The combinations of native words which yield such impressive results in other languages are not possible in English; and, in any case, it seems only reasonable that technical words should be of such a nature, in respect of their etymology, as to be available for universal use.

I have already (loc. cit. 1897) translated Spengel's "Genitalflügel" into genital pleurae. More important is the rendering of Spengel's "Eicheldarm," since this involves matter of controversy. It was Bateson who first advocated the view that this structure is related to the notochord of the Vertebrates, and he, very naturally, called it notochord. The notochord of the Chordata is a structure with which we are all familiar and it is capable of exact definition. What has been called notochord in the Enteropneusta does not correspond with this definition except in its capacity of skeletal product of the gut-wall. A special designation is therefore necessary, and the name I propose for it is stomochord, the first half of the word indicating its relation to the buccal cavity, and the second half indicating its resistent, chord-like character (cf. Pl. XXVI. Fig. 4). This term involves no sacrifice of conviction whatever, since it leaves the question of the morphological relationships of the structure to which it refers quite open.

The stomochord is not the only skeletal product of the gut-wall in the Enteropneusta. Spengel described in Pt. minuta a "kielförmiger Fortsatz des Darmepithels" on the ventral side of the caudal region. Hill has found the same structure in Pt. hedleyi, describing it as a "long and high keel-like process." I have found it in Pt. flava, Pt. carnosa n. sp., and in Pt. ruficollis n. sp. It is a very remarkable structure indeed and deserves to be called a pygochord.

Spengel's longitudinal "Grenzwülste" which characterise the lines of demarcation of the branchial portion of the gut from the esophageal portion in Ptychoderidae are likewise structures to which I shall attribute a peculiar significance. They are the parabranchial ridges.

#### TAXONOMY.

Spengel indicated clearly in his Monograph that the Enteropneusta are divisible into three families, but he did not carry the matter beyond the point of naming one family, viz., the Ptychoderidae. The deficiency may be supplied by naming the three families as follows: I. Ptychoderidae, II. Spengelidae, and III. Balanoglossidae.

The following tabulation may serve as a synopsis of the

#### FAMILIES AND GENERA OF ENTEROPNEUSTA.

## FAMILY I. PTYCHODERIDAE, Spengel.

Proboscis usually shorter than collar; cornua of nuchal skeleton do not extend backwards beyond the middle of the collar; dorsal unpaired roots unite the medullary cord of the collar with the epidermis; efferent vessels of proboscis united in one transverse plane by a circular vessel with the ventral blood-vessel of the collar; peripharyngeal space containing circular muscles completely surrounds the wall of the throat continuously up to the level of the buccal orifice; perihaemal cavities do not contain transverse muscles; circular muscles outside the longitudinal muscles usually present in body-wall of trunk; genital pleurae well-developed or vestigial; lateral septa carrying the genital blood-vessels present; external liver-saccules present (except in Pt. ruficollis n. sp.).

GENUS. PTYCHODERA Eschscholtz, char. emend. Spengel.

With the characters of the family.

A. Gill-slits opening freely and directly to the exterior.

SUBGENUS i. CHLAMYDOTHORAX, Spengel.

Genital pleurae with ventral origin.

Ex. Pt. flava Esch., Pt. erythraea Spengel, Pt. bahamensis Spengel.

B. Gill-slits opening into pouches which discharge to the exterior by dorsal gill-pores.

Subgenus ii. Tauroglossus, Spengel.

Genital pleurae with dorsal origin.

Ex. Pt. aperta Spengel, Pt. clavigera (Delle Chiaje), Pt. gigas (Fr. Müller), Pt. aurantiaca (Girard), Pt. australiensis Hill, Pt. carnosa n. sp., Pt. biminiensis n. sp., Pt. jamaicensis n. sp.

Subgenus iii. Ptychodera, s. str., Spengel.

Genital pleurae vestigial, reduced to ridges.

Ex. Pt. minuta (Kow.), Pt. sarniensis (Koehler), Pt. hedleyi Hill, Pt. ruficollis n. sp.

## FAMILY II. SPENGELIDAE, nov. fam.

Proboscis longer than collar; stomochord produced anteriorly into a long vermiform process; cornua of nuchal skeleton extend to posterior region of collar; roots absent or vestigial; efferent vessels of proboscis pass obliquely downwards to posterior end of collar to unite with the anterior end of the ventral vessel of the trunk; peripharyngeal spaces separate, vestigial or absent; perihaemal cavities contain transverse muscles; the layer of circular muscles in the body-wall lies inside of the longitudinal muscles; genital pleurae and lateral septa, absent; external liver-saccules present or absent.

A. Right and left peripharyngeal cavities present; synapticula present.

# GENUS 1. SCHIZOCARDIUM, Spengel.

Ventral septum of proboscis extends to end of vermiform process; external liver-saccules present; medial gonads absent; pericardial auricles highly developed; œsophageal portion of branchial sac reduced to narrow hypobranchial band.

S. brasiliense, Spengel. S. peruvianum, Spengel.

# GENUS 2. SPENGELIA, Willey.

Ventral septum of proboscis does not extend to the vermiform process; external liver-saccules absent; medial gonads present or absent; pericardial auricles reduced; dermal pits in the genital region; cesophageal portion of branchial sac present as a deep groove.

S. porosa, Willey. S. alba, n. sp.

B. No peripharyngeal cavities and no synapticula.

# GENUS 3. GLANDICEPS, Spengel.

Ventral septum of proboscis, external liver-saccules and medial gonads, as in Spengelia; pericardial auricles rudimentary; esophageal portion of branchial sac reduced to a broad hypobranchial tract.

G. talaboti (Marion), G. hacksi (Marion), G. abyssicola, Spengel.

#### FAMILY III. BALANOGLOSSIDAE n. n.

It is not easy to define this family in terms similar to those employed in the definitions of the two preceding families, because the anatomical characteristics are chiefly of a negative nature.

The most important properties of the members of this family may be summed up as follows:—Boreal forms; with large eggs; developing directly (i.e. without a pelagic larva).

Stomochord without vermiform process; roots absent; cornua of nuchal skeleton, efferent vessels of proboscis and perihaemal cavities, as in Spengelidae; peripharyngeal spaces present or absent; no circular muscles in body-wall of trunk-region; synapticula absent; external liver-saccules absent.

# GENUS. BALANOGLOSSUS (Delle Chiaje).

With the characters of the family.

# Subgenus 1. Balanoglossus s. str. Spengel.

Proboscis short; proboscis-pores paired; peripharyngeal spaces absent; medial gonads present.

B. kupfferi v. Willemoes-Suhm. B. canadensis Spengel.

## SUBGENUS 2. DOLICHOGLOSSUS Spengel.

Proboscis very long; proboscis-pore unpaired; peripharyngeal spaces¹ present; medial gonads absent.

B. kowalevskii A. Agassiz. B. mereschkowskii Nic. Wagner. B. sulcatus Spengel.

#### SYSTEMATIC DESCRIPTION OF SPECIES:

#### FAMILY. PTYCHODERIDAE.

GENUS. PTYCHODERA.

## SUBGENUS 1. Chlamydothorax.

# 1. Ptychodera flava Eschscholtz.

Eschscholtz, Fr.<sup>3</sup> (1825) Bericht über die zoologische Ausbeute der Reise von Kronstadt bis St Peter und Paul. Oken's Isis, p. 740.

Spengel, J. W. (1893), Die Enteropneusten (Monograph, p. 190).

Willey, A. (1897), On Ptychodera flava Esch., Q. J. M. S., Vol. XL., p. 165.

Hill, J. P. (1897—8), The Enteropneusta of Funafuti, Memoirs Aust. Mus. III. p. 205 and p. 335.

Spengel points out that this was the first Enteropneust that was ever mentioned in literature, the original description and name having fallen into complete oblivion until rescued by Carus in his "Prodromus Faunae Mediterraneae." My observations upon this form, as a result of which I showed that it belongs to the subgenus Chlamydothorax, were the first to be made since 1825. It is closely allied to its congeners, Pt. erythraea Spengel and Pt. bahamensis Spengel, from both of which it differs in certain minor details, especially in the matter of the proboscis-pores.

<sup>&</sup>lt;sup>1</sup> The peripharyngeal spaces, as described by Spengel in B. kowalevskii, contain both circular and longitudinal muscles. In all other cases where they occur, they contain only circular or transverse muscles.

<sup>&</sup>lt;sup>2</sup> The species of Enteropneusta can usually be distinguished by external characters alone. When a species has once been recognised as distinct, its internal anatomy must be described for itself apart, because nearly allied species often differ very much in details of organisation. No two individuals of a species are exactly alike.

<sup>&</sup>lt;sup>3</sup> For this reference I am indebted to Spengel's Monograph.

#### COLOUR, MEASUREMENTS, AND EXTERNAL FORM.

The colour is a nearly uniform dull yellow, sometimes with a tendency to a brownish tinge. By attentive examination in the fresh condition, it is often possible to distinguish the males from the females by the presence of true brown pigment in the integument covering the testes on the inner surface of the genital pleurae. The yellow monotone is relieved in the hepatic region. The anterior hepatic coeca have a dark, greenish-brown colour; the mid-hepatic coeca are light brown, passing posteriorly into the yellow ground-colour.

The average length of the entire animal, when extended, may be taken at about 5 inches, the larger specimens attaining a length of 7—8 inches. It is a delicate, fragile species.

The most salient character of its external appearance is due to the presence of the enormous pleural lappets, the **genital pleurae**.

As is usual with Ptychoderidae, the proboscis is normally somewhat shorter than the collar; the latter measures on the average 6—7 mm. in length.

Pt. flava exhibits remarkable variation in respect of the length of the branchial region. As a rule in the living animal the length of the perforated pharynx is about equal to that of the proboscis and collar taken together, but it may be both shorter and longer. Two extreme forms are met with, namely, brachybranchiate and macrobranchiate forms. The specimens which I obtained from the islet of Amédée (Isle du Phare), some ten miles out from Nouméa, inside the barrier reef, include a striking series of brachybranchiate forms. Those from the Isle of Pines are on the whole intermediate between the two extremes, while the macrobranchiate variety was found on the weather side of the island of Lifu¹.

According to my measurements of numerous preserved specimens, those from the Isle of Pines range from about 6 mm. to about 15 mm. in length of branchial region. Specimens from Lifu range up to as much as 29 mm. in length of branchial region, the combined length of proboscis and collar in this case measuring about 12 mm. When the genital pleurae of such an individual are spread out nearly flat, so as to completely expose the long, perforated pharynx, it forms a most striking object (see Pl. XXVI. Fig. 2).

The length of the branchial region is of systematic importance in the case of other species, and the variation of Pt. flava in this respect is therefore of particular interest, since, according to the opinion which I expressed in my previous account of this species, it appears, on the whole, to represent the most primitive Enteropneustic type at present known.

The **postbranchial portion** of the trunk intervening between the branchial and hepatic regions is, as a rule, somewhat shorter than the branchial region, very much shorter in the macrobranchiate forms. In most Enteropneusta this intermediate tract constitutes the **genital region** proper, but cannot be so designated in this and in allied species, because the gonads are entirely restricted to the genital pleurae.

<sup>&</sup>lt;sup>1</sup> Individuals which have regenerated the anterior portion of the body resemble the brachybranchiate variety.

For some distance behind the branchial region, the annulations of the dorsal body-wall (apart from the genital pleurae) are obscure. Gradually, as we proceed backwards, these annulations become more pronounced until they form prominent ridges with deep interannular depressions. Passing still further backwards, the ridges become larger until they form pro-eminent lobes, which are the **external hepatic saccules** (Pl. XXVI. Fig. 1).

The anterior hepatic saccules, which are dark green in colour, have a smooth surface. The mid-hepatic saccules are the largest, are coloured a light brown, and their anterior and posterior faces are distinctly ribbed. The posterior saccules have, as already mentioned, the usual yellow ground-colour, and pass behind imperceptibly into the annular ridges of the abdominal region.

The **caudal region** can be readily distinguished from the abdominal region by the greater compactness and regularity of the annular dermal ridges, by its consequently smoother surface, and, above all, by its rigidity, which is no doubt in great part due to the presence of a remarkable skeletal derivative of the median ventral wall of the gut, which I have called the **pygochord**. In Plate XXVI. Fig. 1, the caudal end of the body is represented as bent at a sharp angle upon the flaccid abdominal region, a condition often met with in preserved specimens.

## PROBOSCIS.

## CAVITY OF PROBOSCIS: DORSAL AND VENTRAL PROBOSCIS-CANALS.

In front of the basal and central organs of the proboscis there is a median cavity, which is sharply demarcated by the presence of a characteristic peripheral aponeurosis, formed by closely-felted fibres of connective tissue, which is more strongly developed on the dorsal than on the ventral side of the central cavity. This aponeurosis sends out interradial processes between the radially disposed bundles of the longitudinal musculature.

If the proboscis be tipped up so as to expose the ventral surface of its neck, a more or less lobulate or **racemose organ**, projecting freely into the buccal cavity, is brought into view. It is still better seen after opening the collar by a ventral incision, as shown in Pl. XXVIII. Fig. 1 a.

This organ is a special development of the ventral coecal prolongation of the proboscis-cavity, the walls of which assume a characteristically lobed structure. In *Pt. erythraea* Spengel has described and figured a corresponding structure, the lobulation of which is much more complicated than in *Pt. flava*, the lobes being numerous and close-set, producing the appearance of a **corymbose organ** (blumenkohlähnlich).

Here it may be remarked that Pt. erythraea is altogether a larger species than Pt. flava.

The **ventral coecum** of the proboscis is produced by the union, behind the free edge of the ventral septum, of the two ventral proboscis-canals, which, in their turn, result from the subdivision of the proboscis-coelom into dorsal and ventral moieties by the transverse coecal expansion of the stomochord. The latter encroaches so much on

the limits of the proboscis-cavity as to entirely displace the lateral portions of the cavity, thus giving rise to two pairs of canals, namely, the **dorsal canals** and the **ventral canals** (cf. Pl. XXX. Fig. 25). The former are associated with the proboscispores and the latter terminate in the ventral coecum of the proboscis (Pl. XXVIII. Figs. 2—3).

As indicated above, the partition between the ventral canals is formed by the ventral septum of the proboscis, which, as in most but not in all species of Enteropneusta, has free anterior and posterior borders<sup>1</sup>. The septum dividing the dorsal canals is formed by the dorsal wall of the pericardium (Herzblase) which reaches the basement membrane of the epidermis (cf. Pl. XXX. Fig. 25 h).

The anterior border of the ventral septum is nearly vertical, usually with a slight backward inclination, but no doubt this inclination would vary under different conditions of contraction. The septum extends a short distance in front of the region of the coecal dilatation of the stomochord, but stops far short of the anterior end of the latter.

In front of the septum, the stomochord is held in position largely by the median dorso-ventral muscles of the proboscis.

## PROBOSCIS-PORES.

Pt. flava is distinguished by the constant occurrence of paired proboscis-pores<sup>2</sup>, which, however, differ from one another in their relations to the coelom of the proboscis. As I attach great importance to these structures I will describe my observations in some detail.

The proboscis-pores, by which the dorsal proboscis-canals discharge to the exterior, are interesting in this species on account of the variations which they exhibit. It is important, however, to bear in mind the fact that a dorsal canal does not lead directly to the corresponding proboscis-pore, but communicates first with a terminal bladder-like dilatation lined by ciliated columnar epithelium. The communication between the canal and its terminal vesicle is effected by the intermediation of a narrow connecting tube, which proceeds from the posterior dorsal angle of the coelomic canal. There are, therefore, four structures to be considered, namely, (1) the dorsal coelomic canal, (2) the connecting tube (coelomic pore), (3) the terminal (ectodermal) vesicle, and (4) the proboscis-pore. The terminal vesicle is the Eichelpforte of Spengel, who identifies it with the ciliated excurrent canal or pore-canal of the anterior coelomic vesicle (Wassersack) of Tornaria.

I now pass on to a selected serial account of my observations on these structures, based on serial sections through different individuals.

<sup>&</sup>lt;sup>1</sup> Spengel has shown that there is no posterior free border of the ventral septum in Glandiceps and I find the same condition in Spengelia.

<sup>&</sup>lt;sup>2</sup> Mr J. P. Hill, who has himself made some observations on *Pt. flava* to which I shall have occasion to refer, first saw the paired proboscis-pores of *Pt. flava* in preparations of his own made from material collected by Mr Charles Hedley in Funafuti.

<sup>&</sup>lt;sup>3</sup> In some other species, e.g. Pt. minuta [Spengel] and Pt. australiensis Hill, the proboscis-pores vary greatly but not in the same way as those of Pt. flava. In Pt. hedleyi, Hill has described paired proboscis-pores which open nearly or quite coincidently in the middle line.

Series i. The bulk of the right dorsal canal ends in the chondroid tissue in advance of the termination of the left canal. Before ending it gives off a connecting tube, which proceeds backwards as a solid cord of cells, finally expanding again into the hellow terminal vesicle which is like that of the left side, but smaller. This vesicle opens to the exterior, on the right side, by a small pore in the same transverse plane as the much larger pore of the left side (Pl. XXVIII. Fig. 2).

On the left side the connecting tube is not solid, the terminal vesicle being in free communication with the left dorsal canal.

- Series ii. The right dorsal canal communicates with a wide terminal vesicle by a narrow connecting tube, whose lumen is occluded. The terminal vesicle opens to the exterior by the right proboscis-pore. On the left side there is no definite connecting tube at all. The left dorsal canal comes to an end in the chondroid tissue, into which it gives off numerous islets of cells, whose presence produces the cartilage-like appearance of the chondroid tissue. There is no cord of cells which can be selected from among these cellular islets as being the representative of a connecting tube. Nevertheless, there duly occurs, on the left side, a terminal vesicle which is not very much smaller than the corresponding structure on the right side, and opens to the exterior by a sinistral pore in the same transverse plane as the right proboscis-pore.
- Series iii. The condition observed here resembles the preceding, except that the right vesicle is in open communication with the right dorsal canal. The left terminal vesicle is hardly any smaller than the right, but its connecting tube is drawn out into a solid or sub-solid cord.
- Series iv. The right terminal vesicle is in open communication with the right dorsal canal. There is also a terminal vesicle and pore on the left side, but the vesicle is not in open communication with the left dorsal canal, the connecting tube being discontinuous and vestigial.
- Series v. Both end-vesicles communicate with their corresponding dorsal canals of the proboscis-coelom, but the left vesicle is rather larger than the right.
- Series vi. Both end-vesicles end solid internally towards the coelomic canals; the right vesicle is larger than the left.

From the above it will be seen that *Pt. flava* possesses paired terminal vesicles and paired proboscis-pores, but those of one side, either right or left, are larger than those of the other. The larger vesicle, whether it is on the right or on the left side, usually retains more or less of a functional communication with the corresponding dorsal canal. The smaller vesicle, on the contrary, shows a distinct tendency to become disconnected with or emancipated from the coelom of the proboscis.

Finally, it is to be noted that in this species the terminal vesicles of the dorsal canals do not open to the exterior by a narrow minute pore, but they usually open bodily by a wide orifice, equal in breadth to their own diameter. These pores can be easily seen in situ in uninjured specimens.

#### STOMOCHORD, PERICARDIUM AND GLOMERULUS.

The behaviour of the stomochord at its distal free extremity, and its relations with the pericardium and glomerulus at this point, are of importance both morphologically and systematically. In *Pt. flava* the stomochord is attenuated at its distal end, being drawn out into a narrow, solid, cellular cord, with which the pericardium and glomerulus are exactly coextensive. The pericardium, like the stomochord, has a simple, pointed anterior extremity.

These three structures (stomochord, pericardium and glomerulus) constitute together the **central complex** of the proboscis. Corresponding to the ventral septum of the proboscis there is, as already mentioned, on the dorsal side a hollow septum, formed by the pericardium, reaching up to the dorsal integument. Its anterior point of union with the basement-membrane of the epidermis, or, in other words, the point (regarding from behind forwards) at which the pericardium ceases to reach the skin, and commences to stretch with a gently inclined free dorsal border to the anterior tip of the stomochord, is far removed from the distal end of the central complex, occurring slightly in front of the level of the anterior free edge of the ventral septum.

The cavity of the pericardium, in the preparations examined by me, is rarely completely filled up by proliferation of its endothelial lining, although the extent to which such proliferation has occurred varies in different specimens. Perhaps it varies at different ages or different periods. In one specimen the anterior end of the pericardium was practically filled with a spongy, reticulate tissue.

The **median septum** of the proboscis is principally formed by what Spengel has described as the dorso-ventral muscle-plate. Its relations to the central complex are of some systematic importance. In *Pt. flava* the median septum is essentially coextensive with the central complex, and does not extend in front of the latter.

The **stomochord** of the Enteropneusta may be resolved into three distinct regions, each of which may present features of diagnostic value. These are (1) the anterior or interglomerular region, (2) the middle or coecal region, and (3) the posterior or nuchal region.

In the Spengelidae the anterior portion is produced into a long, vermiform process, but in other Enteropneusta it is, generally speaking, coextensive with the glomerulus.

If we examine the stomochord of *Pt. flava* from before backwards we find that the anterior attenuated cellular cord passes gradually into a wider portion, with stellate lumen; the stomochord then gradually attains a certain thickness in the dorso-ventral direction, so that, in section, it appears oval or elliptical in shape; the lumen meanwhile becomes indefinitely subdivided. Farther back, near the commencement of the ventral septum, the lumen becomes single and well-defined, and the transverse diameter of the stomochord nearly equals its dorso-ventral diameter.

The coecal dilatation (i.e. the ventral "Blindsack" of Spengel) which characterises the middle region of the stomochord has no continuous transverse lumen in adult examples of Pt. flava, but there may be a trace of such a lumen in a more or less occluded condition. The lateral portions of the lumen appear as paired diverticula from the principal lumen.

<sup>1</sup> In some species, rather more so than in Pt. flava (e.g. Pt. ruficollis and in Spengelia), the lateral portions

Behind the coecal region the stomochord quickly loses its chorda-like character, and no doubt also its rigidity; its function as a supporting organ being, in this region, entirely usurped by the nuchal skeleton. It tends, at the commencement of the nuchal region, to diminish in size up to a certain point, always, however, maintaining its integrity and its lumen (Pl. XXVIII. Fig. 3). Its ventral wall becomes progressively thinner, and, some distance in front of the bifurcation of the nuchal skeleton, the stomochord begins to widen out into the characteristic flattened terminal portion, which finally opens freely into the buccal cavity.

#### NUCHAL SKELETON.

This structure is sometimes referred to as the collar-skeleton, sometimes as the proboscis-skeleton, and Spengel calls it the Eichelskelet.

As the mass of it lies in the narrow neck which joins the proboscis to the collar, while the cornua lie in the collar and keep the mouth permanently open, the above seems to be the most appropriate designation.

There are at least six features of the skeleton to be taken into account, namely, (1) Cupule (Endscheibe or Trichter of Spengel), (2) Body, (3) Crest, (4) Alary processes, (5) Carina or Keel (Kiel or Zahn of Spengel), and (6) Cornua (Schenkel of Spengel).

The cupule embraces the posterior end of the ventral coecal dilatation of the stomochord (Pl. XXVIII. Fig. 2). In *Pt. flava* it is quite shallow, passing abruptly into the solid body of the skeleton. The body in its anterior portion is massive, laterally compressed, sub-rectangular, and produced along the dorsal middle line into a prominent acuminate crest, which projects into the ventral wall of the stomochord. The crest varies, however, in the degree of its development and is sometimes obsolete.

In the mid-region of the body of the skeleton, an accessory skeletal element is added to the main body in the form of a transverse arcuate bar produced at the sides into alary processes, and embracing the dorsal side of the ventral coecum of the proboscis.

In fact, in Pt. flava, as in Pt. erythraea described by Spengel, there is no keel along the ventral side of the nuchal skeleton, its place being occupied by the enlarged ventral coecum of the proboscis. Behind the alary processes the body of the skeleton becomes subtriangular in section, the base of the triangle being directed dorsally and the apex ventrally (Pl. XXVIII. Fig. 3). Immediately in front of the orifice of communication between the stomochord and the buccal cavity, the body of the skeleton becomes bisected, and from this point the cornua begin to diverge.

As in all species of *Ptychodera* the cornua, which lie on each side in a fold of the epithelium of the throat, do not extend backwards beyond the middle of the collar-region.

of the dilated region of the stomochord appear as distinct lateral pouches and are described below under that designation (cf. Pl. XXX. Fig. 25).

<sup>&</sup>lt;sup>1</sup> For full treatment of the nuchal skeleton in its capacity of derivative of the basement-membrane, with proof of its dual origin from stomochord and epidermis as shown by the lines of stratification, etc., see Spengel's Monograph, p. 487 et seq.

#### COLLAR.

#### Collar Nerve-Cord and Roots.

The dorsal nerve-cord in the collar of Pt. flava is a true medullary tube, possessing a continuous central canal which communicates with the exterior, in front and behind, by the anterior and posterior neuropores. In Pt. minuta and in many other species, the lumen of the collar nerve-cord is broken up into a large number of separate medullary cavities. The possession of a continuous axial canal is particularly characteristic of the subgenus Chlamydothorax, and I regard it as most certainly representing the more primitive condition. Such a continuous central or axial canal in the medullary tube of the collar-region, occurs exclusively among the Ptychoderidae, namely, in all the species of the subgenus Chlamydothorax, and in certain other isolated cases, e.g. Pt. sarniensis, Pt. hedleyi, Pt. aperta and Pt. ruficollis n. sp.

The collar nerve-cord is united at intervals with the epidermis by means of unpaired dorsal roots in all Ptychoderidae. These roots are either solid or contain a lumen communicating with the central canal.

I attach special significance to these roots, and will therefore give a serial account of my observations.

Series i.¹ The first root arises shortly behind the orifice of the stomochord as a hollow diverticulum from the medullary tube to the right of the median line, and runs for some distance horizontally backwards, so that in transverse sections through the entire animal the root is also cut transversely to its long axis.

The second root is also hollow, and arises nearly in the median line in front of the point at which the first root meets the epidermis. It is also directed backwards, accompanying the anterior free edge of the dorsal septum of the collar. The first root maintains its calibre until it passes into the epidermis, while the second root becomes somewhat attenuated towards its distal end, although it retains its minute central lumen to the end.

The third root is obviously vestigial in its nature. It appears as a solid bud from the dorsal wall of the medullary tube in the middle line, lying in the dorsal septum. Immediately after its origin its calibre abruptly diminishes almost to vanishing point and in this attenuated portion there are no nuclei. This root likewise has a backward course. When nearly half-way between the medullary tube and the epidermis, its diameter resumes the normal size and a central lumen appears.

Series ii. The first root has a hollow origin and is very slightly oblique, running almost directly from medullary tube to epidermis, so that in one section it is united to the former at its proximal and to the latter at its distal end. It is not a simple cylindrical root but is triangular in shape, the apex of the triangle being its insertion in the epidermis, and the base of the triangle its elongated origin from the medullary tube. The anterior side of the triangle is directed backwards and the

<sup>&</sup>lt;sup>1</sup> Series i—v refer to series of sections through different specimens which do not necessarily correspond with those given on p. 231.

posterior side forwards, reckoning from the base. Moreover, the posterior side coincides with the anterior free edge of the dorsal septum.

The second root is likewise hollow at the base and very slightly oblique in its course from medullary tube to epidermis.

Series iii. The first root is hollow and runs along the anterior edge of the dorsal septum. The second root is hollow and arises close behind the first root from a common neural crest (Pl. XXVIII. Figs. 4a-4c). The third root is hollow and smaller than the preceding. All are directed somewhat obliquely backwards. In describing these roots as hollow, I refer particularly to their origin as hollow diverticula from the medullary tube. In some cases the lumen appears to be broken up into discontinuous portions towards the distal end of the root.

Series iv. The first root is almost entirely solid at its origin, but there is a slight indication of pouching at its base. There are disconnected traces of a lumen in the root itself. This root is large and runs horizontally backwards for a relatively long distance. It is anterior to and independent of the dorsal septum and has not an extended neural crest for a base.

The second root is also solid, narrower and shorter than the first; it accompanies the anterior edge of the septum.

Series v. The first root has a median origin and is hollow, running obliquely backwards along the anterior free edge of the dorsal septum. The second root is also median and hollow like the first, and comes off from the medullary tube before the first root has reached the epidermis.

The above observations may be summarised by saying that in Pt. flava, the nerveroots of the collar are few in number but vary in number, length, course and calibre; sometimes they arise from a common neural crest<sup>1</sup>; sometimes they arise to one side of the middle line instead of being quite median; and, they are primarily hollow.

#### VENTRAL SEPTUM OF COLLAR.

There is no ventral septum in the collar of Pt. flava. Although the complicated longitudinal vascular plexus along the ventral side of the throat causes an extensive fold of the basement-membrane, it does not reach across the collar-cavity to the basement-membrane of the ventral epidermis. The two halves of the collar-cavity are therefore in free communication below the ventral vascular fold. In some cases the ventral septum persists through a great part of the collar-region as in Pt. sarniensis; in others it is restricted to a narrow tract at the posterior end of the collar as in Glandiceps talaboti. It is also largely persistent in Spengelia (see below). Spengel has pointed out that neither the dorsal nor the ventral septum of the collar is ever complete; but both septa when present, always have a free anterior margin. Perhaps the vascular fold suspended from the basement-membrane of the throat-epithelium in

<sup>&</sup>lt;sup>1</sup> In other cases, besides that mentioned above in connection with Series iii., successive roots come off from a common crest but not, as a rule, so strikingly as appears in that series.

Pt. flava is to be interpreted as an incomplete ventral septum; but there is reason for supposing that it would be more correct to treat the ventral vascular complex and the ventral septum as two distinct structures which may or may not, coincide.

#### COLLAR CANALS AND PORES.

The collar-canals (Kragenpforten) of Pt. flava vary so much in their length and in the character of the dorsal wall, that they are of little use for diagnostic purposes. The dorsal wall is folded into the lumen of the canal by a simple tongue-like plication. This dorsal fold is always deep, but is larger in some cases than in others and resembles roughly the condition described and figured by Spengel for Pt. minuta and Pt. aperta.

Each canal opens internally into the collar-coelom by a ciliated semilunar funnel. Sometimes the canal is so short that its ventral wall is fused with the epithelium of the first gill-pouch in the same transverse plane with the funnel. More usually a tube of some length with deeply infolded dorsal wall intervenes between the internal funnel and the external pore. The latter opens into a special dorsal section of the first gill-pouch. The first gill-slit of all Enteropneusta (unlike Amphioxus) is complete, and provided with a tongue-bar like the rest. The first septal bar is therefore confluent with the epithelium of the throat or collar-gut. The collar-pore opens into the dorsal angle made by the first septal bar with the posterior edge of the collar, this angle being tucked in for some distance beneath the collar-rim (Pl. XXVIII. Fig. 5).

There are therefore three portions of a collar-canal to be considered, namely, (1) the funnel, (2) the tube, and (3) the pore. The tube appears to be largely formed by intercalary growth, between the funnel and the pore, during the life of the animal.

#### TRUNK.

#### Branchial Region.

I hope by this time that the fact of the existence of Enteropneusta with a free, exposed pharynx, has sunk into the mind of the reader (Pl. XXVI. Figs. 1 and 2).

In horizontal sections it appears that the first two gill-clefts do open into gill-pouches owing to the protrusion of the anterior end of the pharynx within the posterior limits of the collar, but the bulk of the gill-slits open freely to the exterior, a fact which might also be expressed by saying that the gill-pouches are confluent.

In sections through this region Pt. flava is apparently distinguishable from the other two species of the subgenus Chlamydothorax, as described and figured by Spengel, in respect of the relative cubic capacity of the branchial and esophageal portions of the pharynx. In Pt. erythraea the esophageal division predominates over the branchial division; in Pt. bahamensis the two divisions are nearly equal; finally, in Pt. flava the branchial predominates over the esophageal division (Pl. XXVIII. Fig. 6).

The line of demarcation between the bases of the gill-bars and the œsophageal epithelium is occupied, as in all Ptychoderidae, on each side by a prominent longi-

tudinal ridge, which Spengel has called the "oesophageale Grenzwulst." These ridges are what I call the **parabranchial ridges**, and I am disposed to attach high morphological importance to them. They are certainly important structures anatomically, as may be best seen by simple dissection (Pl. XXVIII. Fig. 1a). They are co-extensive with the gill-slits, and, at the anterior end of the pharynx, they are seen to pass round into the median dorsal epibranchial band. As shown in Pl. XXVIII. Fig. 8, the parabranchial ridges are nothing else than the confluent thickened ventral walls of the gill-clefts.

## GENITAL PLEURAE AND LATERAL SEPTA.

The genital pleurae of Pt. flava resemble those of the two species of the subgenus Chlamydothorax which were described by Spengel, in their extreme ventral origin. So low is their origin that they leave the pharynx quite free and exposed, so that the gill-slits open laterally in their entirety directly to the exterior. The pharynx remains erect owing to the rigidity of its walls, which is effected by the skeletal supports in the gill-bars. The latter are markedly arcuate with the convex side directed outwards so that the pharynx presents the appearance of a sub-cylindrical body with the annular septal branchial arches and intervening slits. The tongue-bars lie far inwards towards the cavity of the pharynx, and so are not visible in external view in preserved specimens. In all Ptychoderidae the tongue-bars have a more internal position than the septal bars.

The gill-clefts are crossed by solid connecting rods or synapticula, so that the result is a branchial basket (Pl. XXVIII, Fig. 8).

The average number of synapticula on each side of a tongue-bar is 10—12; but there may be as many as 18—20 in the macrobranchiate forms. The plication of the outer wall of the tongue-bar, which has been noted in so many cases, is not a constant feature in *Pt. flava*. It not only varies in successive bars but at different levels in the same bar.

In most Enteropneusta the external openings of the gill-slits are reduced to small pores, which occur in linear series on the dorsal side of the animal, on each side of the middle line, at the base of a longitudinal groove known as the branchial groove; in such cases the gill-slits no longer open directly to the exterior but into special branchial pouches which, in their turn, discharge to the exterior by the aforesaid gill-pores.

The genital pleurae, in addition to their primary function of bearing the gonads, serve also the accessory function of protecting the branchial basket. They can be folded over the latter so as to meet and even overlap in the dorsal middle line, and, when so carried, they form a complete temporary peribranchial chamber, only open posteriorly where the pleural folds divaricate. On the other hand they can be spread out laterally in the plane of the ventral side of the body. They are extremely mobile structures, and attain their maximum development about the middle of the branchiogenital region.

Towards the hepatic region the pleurae diminish gradually in size and also attain a more dorsal position. They enclose the more anterior liver-saccules, and are finally

continued as a low ridge immediately outside of and below the liver-saccules, through about four-fifths of the hepatic region (Pl. XXVIII. Fig. 1). This mode of termination of the genital pleurae is, in the main, characteristic of the subgenus *Chlamydothorax*. Inseparably associated with the genital pleurae are the **lateral septa** which carry bloodvessels to the gonads. So far as Spengel's account of them in *Pt. erythraea* goes they have the same proximal origin and distal insertion in *Pt. flava* (Pl. XXVIII. Figs. 6 and 7). But Spengel does not state the important fact that, whereas in most cases the lateral septa are limited in their anterior extension, in *Chlamydothorax* (judging by *Pt. flava*) they are coextensive, in front as well as behind, with the genital pleurae.

This fact explains the meaning of the lateral septa as vascular folds of the base-ment-membrane accompanying the pleural expansions or outgrowths of the body.

In the branchial region of *Pt. flava* the lateral septa arise from the basement-membrane of the epidermis on the medial side of and dorsal to the angle formed by the junction of the genital pleurae with the body-wall. Peripherally they are inserted again into the basement-membrane of the epidermis at the free edges of the genital pleurae. Behind the pharynx their line of origin is transferred from the basal membrane of the epidermis to the basement-membrane of the wall of the gut. In the mid-hepatic region their line of origin occurs alternately in the side of the hepatic diverticula, and in the basement-membrane of the epidermis in the intersaccular intervals (Pl. XXIX. Fig. 14).

In a form like Pt. minuta with reduced genital pleurae the causal relations of the lateral septa and genital pleurae are obscured, and the portion of the coelom enclosed by the septa appears as a pouch on each side ending coecally in front and was so interpreted by Spengel. Pt. flava shows conclusively that the lateral septa belong to the pleural system, and no pouching whatever (apart from the pleural outgrowths) of the body-cavity has taken place. This should be particularly noted, as this is a tangible example demonstrating how that Pt. minuta is a misleading form to take as a basis for the interpretation of the Enteropneustic organisation (cf. Spengel, Mon, p. 60).

#### BRANCHIOGENITAL TRANSITION.

The region of the body which lies between the branchial and the hepatic regions has been called the **genital region** by Spengel; but as the gonads generally extend for a greater or less distance into the branchial region, he also applies the term **branchiogenital** to the two regions taken in combination. The intimate relation between branchial and genital regions, which is expressed in this word, is probably of great significance, and will be dealt with in the portion of this memoir devoted to the morphology of the Enteropneusta.

There is no true genital region in *Pt. flara* in the sense in which it occurs in other forms, since the gonads are emancipated from the main body of the animal, being confined to the genital pleurae. It is only therefore in comparison with other forms that the short stretch of body which is intercalated between the posterior end of the pharynx and the anterior end of the hepatic region, can be spoken of as the genital region (cf. Pl. XXVIII. Fig. 2).

Behind the last pair of gill-slits the gut still retains, over a distance of a few millimetres, its division into upper and lower moieties corresponding to the branchial and cesophageal portions. This fact has been already recorded for Pt. flava by Hill (loc. cit. p. 343). A similar condition has been described by Spengel in Pt. erythraea (Monograph, p. 181, Text-figure) and more recently by Hill (loc. cit.) in Pt. hedleyi. In Pt. erythraea Spengel describes the gut in this region as being divided "durch zwei seitlich einspringende Falten in zwei Halbcanäle, einen dorsalen und einen ventralen." In Pt. bahamensis Spengel found the division to be a very unequal one, the dorsal portion occurring as a rather deep furrow, while the ventral portion is much more extensive. In Pt. hedleyi the dorsal moiety is very pronounced and is described by Hill as a dorsal diverticulum possessing a transverse lumen and communicating with the ventral portion of the gut "by a short, laterally compressed stalk"; its high glandular epithelium is thrown into low folds.

I shall refer to this dorsal portion of the gut at the anterior end of the post-branchial genital region as the **postbranchial canal** (Pl. XXVIII. Fig. 7). It is a structure of some diagnostic and morphological importance. In *Pt. flava* new gill-slits arise at the dorsal margins of the postbranchial canal at its anterior end. In *Pt. hedleyi*, as described by Hill, and in *Pt. ruficollis* n. sp. (see below) it is quite independent of, and dorsal to, the most posterior gill-slits.

In Pt. flava the postbranchial canal occurs in direct continuity with the branchial division of the gut. It is lined by a high, smooth deeply staining ciliated epithelium, which passes rather abruptly into the folded epithelium of the ventral division of the gut. Behind the last pair of gill-slits it possesses a narrow vertical lumen with a slight dorsal dilatation, the lumen opening below, throughout its entire extent, into the general cavity of the gut.

With regard to the formation of new gill-slits at the posterior end of the pharynx, I observed in one series that the last gill-pouch of one side opens to the exterior, while the corresponding pouch on the other side is present as a blind diverticulum proceeding from the dorso-lateral margin of the gut, which has not yet come into contact with the epidermis. Nevertheless the tongue bar has commenced to grow down in the form of a slight vascular fold of the dorsal epithelium of the pouch-like diverticulum. This early appearance of the tongue-bar before the perforation of the gill-slit is a fact of importance and is in accordance with what Morgan<sup>2</sup> has observed in Tornaria.

In fact, whereas in Amphioxus the tongue-bars of the gill-slits are of secondary origin and are therefore rightly referred to as the secondary bars, in the Enteropneusta they are of primary origin, and should never be spoken of as secondary bars.

#### GONADS.

The gonads are essentially confined to the genital pleurae, and consist of a great number of separate, more or less lobulated, genital glands, whose arrangement is on the

<sup>&</sup>lt;sup>1</sup> In one specimen I found the cavity of the postbranchial canal to be wide and its walls somewhat coarsely folded in contrast to the epithelial plications which occur in Pt. hedleyi and Pt. ruficollis.

<sup>&</sup>lt;sup>2</sup> T. H. Morgan, "The growth and metamorphosis of Tornaria," Journ. Morph. v., 1891, p. 407.

whole diffuse, although it may be observed that they are disposed in a more or less zonary manner roughly analogous to the epidermal annulations. Of course the gonads are not directly influenced in their topography by the epidermal annulations (although originally I believe the genital zones and epidermal annulations were topographically related), and in mature or sub-mature specimens their ramifications often extend over more than one epidermal zone. The principle of zonulation is directly suggested by the facts which were first described and figured by Spengel in Pt. erythraea and Pt. bahamensis, that the gonads are disposed in many superposed tiers and that the genital ducts occur in numbers in one and the same transverse section. I ought perhaps to explain that the principle of zonary distribution was not present to my mind when I first dealt with Pt. flava, but I have been led to adopt it by subsequent observations. The gonads extend in front to the anterior end of the genital pleurae up to the septum which divides the collar coelom from the truncal coelom, so that they are met with in the same transverse sections with the collar canals.

The shape of the gonads varies greatly in both sexes and also according to the state of contraction or extension of the animal. The fact that, in the male, the integument over the testes on the inner surface of the genital pleurae contains patches of dark brown pigment, has been already referred to (Pl. XXVIII. Fig. 10).

Each gonad is surrounded by a basement-membrane which carries blood-vessels between its inner and outer lamellae (in the manner shown by Spengel to be characteristic of the Enteropneusta), and at the same time serves as a tunica propria. Each gonad, accordingly, has its own duct which perforates the musculature of the inner wall of the genital pleurae, and so brings the tunica propria of the gonad into fusion with the basement-membrane of the epidermis.

The gonads contain actually or potentially a central cavity which may perhaps be regarded as coelomic in nature as opposed to being haemocoelic. It is important to emphasize the fact that in the Enteropneusta the **genital coelom** (i.e. the cavities of the gonads) is quite independent of, and at no time has any connection with the perivisceral coelom.

The gonads contain, in addition to the sexual elements, a large quantity of a fat-like substance consisting of masses of refringent globules of various sizes, which have a great attraction for eosin.

Normally both right and left genital pleurae are fertile and contain an equal complement of gonads. In one series of sections, however, through a male individual, I find that the gonads are only developed in the right genital pleura, the left pleura being sterile. On the left side the gonads, in this case, appear to be in an arrested state of development, being represented by inconspicuous hollow sacs lined by germinal epithelium. There are no fat bodies present, and we may conclude from that that a portion of the germinal epithelium becomes normally employed in the manufacture of nutritive material, while the rest goes to form ova or spermatozoa as the case may be. Such a differential behaviour of the two sides of the body is of interest as indicating a tendency to unilaterality in the matter of the gonads.

In Pt. minuta Spengel says that the fatty material in the gonads is finally quite replaced by ova and spermatozoa; and this is no doubt what takes place in every case,

although in Pt. flava the eosinophile globules occur in great profusion in company with mature ova.

The mature eggs are small, round and subtransparent. They measure '06 mm. in diameter' and, when freshly isolated from the body, are found to be contained in a double-contoured membrane between which and the ovum itself there is an intervening space. The size of the ova in Enteropneusta is particularly noteworthy since it enables us to determine whether any species will develop with or without metamorphosis.

With regard to the nature of the cells which contain and produce the eosinophile globules I cannot add very much to Spengel's observations. Spengel sought in vain for nuclei in these cells in Pt. minuta, but left it doubtful whether certain peripheral flattened nuclei belonged to them or not. In Pt. flava I think I can state definitely that these cells do not contain normal nuclei, for the simple reason that the eosinophile globules themselves are apparently products of nuclear degeneration. The course pursued in this process of degeneration is apparently that of hypertrophy of the nucleolus to which must perhaps be added a multiplication of nucleoli. My interpretation of the appearances presented is that the entire original nucleus undergoes a nucleolar degeneration analogous to fatty degeneration. Spengel points out that these fat-like globules are not fat since they are unaffected by the usual fat-solvents and are also very resistent to caustic potash. He says that sometimes they stain very darkly with haematoxylin and at other times remain quite unstained. This would appear to indicate an ever-changing chemical constitution. Spengel does not seem to have treated them with eosin. In his Taf. XI., Fig. 23 Spengel figures these globules of various graded sizes filling up the cells which contain them. In the text (p. 656) he says, "Bisweilen nimmt eine grössere Kugel die Mitte ein und kleinere umgeben sie." What sometimes happens in Pt. minuta, happens as the rule if not invariably, in Pt. flava.

In this species the normal condition of these nutrient cells at a stage preceding that of their maximum development is shown in Pl. XXVIII. Fig. 11. The large central globule is surrounded on all sides by very much smaller, but otherwise similar, globules. Of course at different stages of growth the contrast in size is not so great as shown in the figure, and I am quite unable to say whether the globules increase in size entirely by intussusception or whether fusion takes place. Spengel could form no opinion as to the relation of these bodies to the sexual elements. As he saw in Pt. minuta and I have seen in female Pt. ruficollis n. sp., the globules disappear at the period of complete maturity. But the eggs retain their small size and, as mentioned above, in Pt. flava ripe eggs coexist in the ovaries with abundant eosinophile globules. In fact this substance appears to serve two functions. The first function, it would seem necessary to assume, would be the nutrition of the growing germ-cells. The second, which later becomes the principal function, is not that of actively nourishing the germ-cells, but of providing an albuminous medium to preserve the germ-cells under the best possible physiological conditions during the final crucial stages of maturation.

That these globule-containing cells, in their original quality of nucleated cells, are in a condition of degeneration, is merely a statement of fact. One of the chief reasons which led me to the above interpretation is that the large central globule is often seen to contain clear refringent inclusions, closely resembling, on a larger scale, analogous inclusions which

<sup>&</sup>lt;sup>1</sup> In my former paper, by a *lapsus calumi*, the diameter was stated to be '006 mm. although the correct magnification was given in the explanation of the plate.

I have observed, in every case, in the normal nucleoli of the germinal vesicles of the mature ova of Pt. ruficollie n. sp. (Pl. XXX. Fig. 34).

The number of eosinophile globules whose chemical nature is unknown is alarmingly on the increase.

If the interpretation which I have suggested at all approaches the truth the globules now under consideration would be composed of a substance allied to pyrenin. It must be added that I have made no observations on the processes of maturation of the germ-cells themselves. This is a subject which presents great difficulties and probably necessitates the employment of a special and elaborate technique.

#### GENITO-HEPATIC TRANSITION.

The genital pleurae with their contained gonads encroach for a considerable distance upon the hepatic region. The first few hepatic diverticula are internal and do not cause elevations of the integument; they are characterised by their much elongated epithelium consisting of closely packed cells with basal nuclei in an approximately even layer, and containing peripheral yellowish-brown intracellular granular deposits.

As they approach the hepatic region the genital pleurae begin to diminish in size and to become more and more dorsal, until at the beginning of the hepatic region they are quite dorso-lateral in origin. They maintain their integrity for some distance, but when the hepatic diverticula commence to cause projections of the integument between the genital pleurae, the latter are, at these successive points, greatly reduced in size, widening out again in the intervals between the saccules. Finally, when the latter become more massive, the genital pleurae are reduced to zero at the level of the saccules and only reappear in the intervals as ridges bounding the interannular depressions between the hepatic lobes (Pl. XXIX. Fig. 14).

The hepatic diverticula of the gut have a very rich blood-supply, the vessels forming a rete mirabile on their walls.

## CILIATED GROOVES OF INTESTINE.

These are longitudinal grooves in the wall of the gut in the hepatic and abdominal regions, which Spengel found to be especially characteristic of the Ptychoderidae. They consist on each side of a narrow tract of richly ciliated epithelium more or less overhung or protected by an epithelial covering-pad developed on the medial side of the groove.

In Pt. flava they are not simple longitudinal grooves but possess metameric sacculations corresponding in the hepatic region to the intersaccular valleys (Pl. XXIX. Figs. 12—14). They commence at the extreme anterior end of the hepatic region, in the region of the genito-hepatic transition, and they extend backwards to the posterior end of the abdominal region. In some places the sacculations of the ciliated grooves approach very close to the epidermis, almost touching the basement-membrane of the latter.

<sup>1</sup> The blood in the vessels round the hepatic epithelium is sometimes coloured a bright refringent yellow.

Sometimes the continuity of the grooves appears to be lost or obscured in the interval between two sacculations.

The covering-pad is especially prominent in the sacculations, and less so in the intervening tracts.

A similar sacculation of the ciliated grooves has been described by Spengel in *Pt. erythraea* (*Mon.* p. 183), where it gives rise to special nodal prominences of the bodywall external to the liver-saccules. These nodal prominences are continued behind the hepatic region.

In Pt. minuta [where there is a ciliated groove on the left side only (Spengel)], Pt. australiensis Hill and Pt. hedleyi Hill, the ciliated grooves lie close to the epidermis, and corresponding with each groove there is a longitudinal epidermal band characterised by the absence of gland-cells.

In Pt. flava the ciliated grooves show through the skin during life but, as Hill has pointed out, there are no glandless epidermal stripes.

In Pt. sarniensis Spengel has described a ciliated groove (Wimperapparat) on the left side only, which however has no relation to, and in fact is far removed from the vicinity of, the epidermis.

## CAUDAL REGION.

This region is above all characterised by the presence of a longitudinal, solid, supporting band, derived from and in continuity with the epithelium forming the median ventral portion of the gut-wall.

This is what I propose to call the pygochord. It is probably of some economic importance to the animal as it is of diagnostic importance to us.

This structure was first described by Spengel in *Pt. minuta* as a remarkable "kielförmiger Fortsatz des Darmepithels," and has since been described by Hill in *Pt. hedleyi* as "a long and high keel-like process, the slightly enlarged ventral end of which overlies the minute ventral vessel."

In Pt. flava it commences at the anterior end of the caudal region as a simple thickening of the ventral wall of the hind-gut which is soon drawn out into a flattened band with dilated distal (ventral) border (Pl. XXIX. Fig. 15 b). As a rule the pygochord retains its connection with the gut-epithelium, but at irregular intervals the basement-membrane is continued across the line of junction so as to completely separate the pygochordal tissue from the wall of the gut. The dilated distal end is sometimes similarly shut off from the rest of the band, and the band itself is sometimes constricted by transverse fusions of the basement-membrane.

Sometimes the band presents a remarkable moniliform appearance due to this fusion of the basement-membrane at different levels (Pl. XXIX. Fig. 15 a).

The pygochord ceases at the anus.

The hind-gut of Pt. flava is surrounded by a very feeble muscularis, while the anus is provided with a light sphincter formed by the circular muscles of the body-wall.

#### OECOLOGY.

Pt. flava occurs in clean loose coral-sand between the tide-marks. It does not burrow to any great extent but frequents the superficial layer of sand, and the meshes formed by the roots of seaweeds and crevices in stones. I have found it in three localities, viz. at the Isle du Phare opposite Nouméa, at the Isle of Pines, and at Lifu. Hill has recorded it from Funafuti and Mr J. Stanley Gardiner brought back a few specimens from the same locality. It is a gregarious species and is usually to be obtained in considerable numbers. As a rule, Pt. flava seems to prefer the weather side of the islands, that is to say the side which is exposed to the prevailing wind. This preference is clearly shown at Lifu, the lee side of which forms a large inlet known as Sandal Bay. I never found Pt. flava on the shores of Sandal Bay, but had to cross over to the opposite side of the island, which is bounded by a continuous fringing reef, to obtain my material.

In a small percentage of specimens there is found a parasitic Copepod which lives in the genital pleurae causing a prominent tumour or gall. I gave a figure of an infected specimen in my former paper on this species (loc. cit.). A similar parasite was found by Spengel in Pt. minuta and named Ive balanoglossi Paul Mayer. In Pt. australiensis Hill found that a similar parasite infested a large proportion of the individuals of the species.

The intimate association of quite distinct species of Enteropneusta is an interesting feature in their distribution. At Funafuti Pt. flava and Pt. hedleyi were taken together by Mr Charles Hedley. At Lifu I took Spengelia porosa in company with Pt. flava and in New Britain Pt. ruficollis n. sp. inhabits the same burrows with Pt. carnosa n. sp.

Pt. flava does not practise autotomy in the same way as this takes place in Pt. carnosa and Sp. alba (cf. Pl. XXVII. Figs. 6 and 9) but it is fragile and excessively prone to laceration. The wall of the hind-gut is well vascularised and the anal orifice may be seen to open and close periodically irrespective of defectation, thus suggesting anal respiration.

## REGENERATION IN PT. FLAVA.

Like Pt. minuta (cf. Spengel, Taf. xxvi. Figs. 14—18) Pt. flava possesses extraordinary powers of regeneration, and the processes involved in the regeneration of the proboscis and collar are unusually instructive, especially if, as Barfurth¹ and others think, regeneration is sometimes (not always) accompanied by atavistic phenomena. Of course the phenomena of regeneration will vary according to the region in which it takes place. For example, if it occurs behind the genital pleurae (Pl. XXVI. Fig. 5 C) the appearances presented are different from those which are exhibited when the regeneration occurs in the region of the pleural folds. It is these latter cases to which I desire to draw particular attention.

The chief facts observed are evident in the figures on Plate XXVI., and it will suffice to point out the principal conclusions derived therefrom. I have confirmed these conclusions as far as possible by sections, some of which are reproduced on Plate XXXII.

- 1. When regeneration occurs in the region of the genital pleurae the collar is regenerated from the pleurae.
- 2. The collar nerve-tube is formed by the fusion of true medullary folds which are differentiated from the pleural folds (Pl. XXVI. Figs. 5 A and 5 B).
- 3. The zones of the collar are differentiated from the annulations of the body-wall (Fig.  $5\ E$ ).
- 4. In regenerating individuals the right and left proboscis-pores are approximately equal. In the specimen shown in Fig. 5 A they were quite equal.
  - 5. In regenerating individuals the lumen of the stomochord is, at first, entire.

For my part I am persuaded that the above facts have an atavistic significance. I do not think there is any reason for regarding the collar as being anything more than a differentiation of the anterior portion of the trunk associated with the cephalisation and regional differentiation in general, which is such a prominent characteristic of the Enteropneusta. This remark refers simply to the collar as such, and not to the pair of body-cavities which form the collar-coelom. These cavities may possibly date much farther back than the collar itself, which is a purely Enteropneustic structure.

As MacBride<sup>2</sup> has shown, homologous coelomic pouches occur in Amphioxus where there is no collar. It is important not to confound the collar with the collar-coelom.

<sup>&</sup>lt;sup>1</sup> Dietrich Barfurth, "Regeneration und Involution" in Merkel u. Bonnet's Ergebnisse der Anat. u. Entwickgesch. Bd. iv. 1894.

<sup>&</sup>lt;sup>2</sup> E. W. MacBride, "The early development of Amphioxus," Q. J. M. S., Vol. xl. 1897-8, p. 589.

In possessing, in such a high degree, the faculty of regeneration, the Enteropneusta differ radically from Amphioxus, which does not regenerate after fracture.

The possibility of regeneration revealing facts of atavistic significance is a matter of great suggestiveness. At the same time, the assertion that any particular process of regeneration is atavistic is always liable to be dismissed as arbitrary. It is very important to bear in mind that regeneration at different regions of the body may be accompanied by different appearances and will yield different information. The atavistic phenomena associated with regeneration carry us farther back than do the phenomena of ontogenetic recapitulation. Although Morgan has found that in *Tornaria* the collar nerve-cord arises by the depression and closure of a medullary groove, yet it could not there be recognised that the medullary folds are metamorphosed derivatives of pre-existing pleural folds. It is practically certain that *Pt. flava* develops through a *Tornaria* stage. No *Tornaria* has ever been seen having two water-pores. On the other hand in a regenerating *Pt. flava* we find a restoration of what must have been the primordial condition, viz. equal paired proboscis-pores.

In the regenerating individual shown in Fig. 5 A, Pl. XXVI., the medullary folds are seen to be widely separated in front and less widely separated behind (cf. Pl. XXXII. Figs. 66—67); in Fig. 5 B the medullary folds are closely approximated and transverse sections reveal the fact that they are actually fused together over a short stretch at the extreme anterior end of the collar (Pl. XXXII. Fig. 68) behind which they are still unfused, the narrow superficial groove leading directly into a wide medullary canal. At this and at the preceding stage there is no free collar-flap in front. In the stage of regeneration shown in Fig. 5 D a median dorsal groove is seen to occupy the posterior two-thirds of the collar region, and in front of the groove is a smooth tract which represents the anterior free collar-flap.

After the closure of the medullary folds the collar continues to grow in length and to project forwards as a free circular fold (collar-flap). The medullary tube must also be involved in the general growth in length and so we find that it extends forwards in front of the dorsal septum which, as in the normal adult, has an anterior free border. Thus although in this specimen (Fig. 5D) the dorsal septum is not coextensive anteriorly with the medullary tube, it is so posteriorly and it presents clearly the appearance of resulting from and representing the raphe of fusion of the medullary folds<sup>2</sup>. Inside this dorsal septum there are cellular remains of the solid plate or keel of ectoderm which is produced by the fusion of the folds (cf. Pl. XXXII. Fig. 68 and Text-fig. 1). Sometimes these remains are in the form of disconnected

¹ Reference is made below to the anterior "Epidermistasche" which Spengel describes in place of the anterior neuropore. In the specimen of Pt. flava shown in Fig. 5D there is no question of an "Epidermistasche" which in other cases may coincide with the neuropore. In this case there is only the true neuropore at the anterior end of the fused medullary folds. The collar-flap projects above and beyond it, but there can be no confusion between the angle formed by the collar with the neck of the proboscis and the neuropore, such as is possible in certain cases.

<sup>&</sup>lt;sup>2</sup> The dorsal septum which, when present, unites the collar nerve-cord with the epidermis, should not be confounded with the dorsal mesentery which primarily separates the two collar-cavities from one another at an early stage. This mesentery is represented in the adult by the median partition between the right and left perihaemal cavities, which carries the dorsal blood-vessel.

débris, while others approximate to the character of roots, of which the first accurately coincides with the anterior free border of the septum. This root is massive and solid at its base and attenuated distally; it occurs in the region of the buccal orifice of the stomochord. The second root is slender, solid at its origin and sub-solid through-



Fig. 1. Portion of transverse section through the middle of the collar of the specimen drawn on Pl. XXVI. Fig. 5D. The section shows the fourth root passing from the dorsal side of the medullary tube to the basement membrane of the epidermis and illustrates the interpretation of the root and the septum in which it lies, as a product of the raphe of fusion of the medullary folds. The superjacent epidermal groove presumably represents what is left of the medullary groove after the closing-in of its lower portion to form the medullary tube (cf. Pl. XXXII. Fig. 68).

out, and does not fuse with the epidermis. The third root is similar except that it meets the epidermis; the fourth root does not fuse with the epidermis, neither does the fifth and last, which is massive and presents disconnected traces of lumen.

These observations may throw a partial light on the origin of the roots as successive differentiations from the raphe of fusion of the medullary folds, but they throw no direct light upon their character of hollow tubes passing from the medullary canal to the epidermis.

## SUBGENUS 2. Tauroglossus.

## 2. Ptychodera carnosa n. sp.

COLOUR, MEASUREMENTS AND EXTERNAL FORM.

This is a giant Enteropneust like *Pt. gigas* and *Pt. robinii*, the latter according to Spengel being the Atlantic form of the Mediterranean *Pt. clavigera*<sup>1</sup>.

TABLE OF COLOUR AND MEASUREMENTS (in mm.).

| Speci-<br>men | . Colour  | Proboscis | Collar<br>length                     | Branchial<br>region      | Genital region  | Inter-<br>mediate<br>tract | Hepatic<br>region | Abdominal<br>and caudal<br>region |
|---------------|---|-----------|--------------------------------------|--------------------------|---|----------------------------|-------------------|-----------------------------------|
| 1             | Rich yellow<br>throughout, faint<br>salmon tinge in<br>genital pleurae          | 6         | 17:5                                 |                          |   |                            |                   | 1                                 |
| 2             | Pale yellow<br>throughout   | 8         | 16                                   |                          |   |                            |                   |                                   |
| 3             | Prevailing colour<br>of branchiogenital<br>region, dark sal-<br>mon or purplish | 10        | 22.5<br>[Max.<br>width<br>behind 16] | 92                       | 160 –170<br>[Width across<br>outspread genital<br>pleurae behind<br>pharynx 35] | 10                         | 106               | About<br>1 foot                   |
| 4             | Genital pleurae<br>with salmon-<br>coloured gonads                              |           | 14<br>[Width<br>9—10]                | 26.5<br>[Width<br>10—12] |   |                            |                   |                                   |
| 5             | Salmon-coloured<br>gonads; collar<br>creamy yellow,<br>darker in centre         |           | 12:5                                 | 29*5                     | 64  |                            |                   |                                   |

The immature eggs are purple and are surrounded by orange-coloured fat-globules, the combination of the two colours producing the salmon tone. As the eggs ripen the pronounced purple coloration is lost and the fatty matter seems also largely to lose its colour, so that the result is a dull neutral tint. Sometimes the prevailing colour of the genital pleurae is dark with a violet tone.

The posterior zone of the collar is sharply differentiated from the other zones. In paler specimens it is intensely white, while in the more richly coloured individuals it is not so conspicuous but always to be recognized.

<sup>&</sup>lt;sup>1</sup> If Spengel is right in regarding *Pt. robinii* as a giant variety of *Pt. clavigera*, it furnishes an interesting analogy with the large Amphioxus (8 cm. long) of the coasts of France as compared with the smaller Mediterranean form.

In the largest specimen whose measurements are given in the above table, the hepatic region commenced with about a dozen brown hepatic coeca, which were followed by a long stretch of foliaceous, dull yellowish saccules, and these again by a still longer gradually decreasing series of brown lobes. The larger saccules are finely digitate or crenulate at their free margins and are quite lamelliform, like the leaves of a book, being extraordinarily flattened antero-posteriorly and closely crowded together.

On the inner surface of the genital pleurae, especially towards the base, are often to be observed numerous white rounded dermal islets.

In some cases the gill-pores may be observed to be surrounded by a rim of brown pigment, and fine lines of the pigment radiate out from the gill-pores to the submedian line<sup>1</sup> in which the genital pores occur.

The proboscis is remarkable for its small size relatively to the capacious collar (Pl. XXVII. Fig. 6). It is probably liable to frequent injury owing to the excessive boring propensities, deep down in heavy volcanic sand, which this species exhibits. Specimens are often obtained in which the proboscis is quite concealed within the collar without betraying any pronounced lacerated surface; so that it probably regenerates very quickly.

The most distinctive external feature of this species is the abrupt ending of the genital pleurae some distance in front of the hepatic region (Pl. XXVII. Fig. 6).

The maximum development of the genital pleurae is behind the branchial region. In front they become much lower as they approach the posterior rim of the collar, and converge towards the middle line. The genital pleurae can not only meet one another in the middle line so as to close in the dorsal nerve-cord and the branchial tract, but they can effect a **mucous junction** with one another. When the animals are preserved during such a mucous junction (which normally is only temporary) the mucus coagulates into a dense leathery band, which is untearable. If one tries to separate the pleurae by force the body-wall ruptures but the mucous coagulum remains entire. No such mucous junction of the genital pleurae is effected in *Pt. flava*.

Sometimes the gonaducal (submedian) line is marked out behind the branchial region by a brown-pigmented groove running along the inner base of the genital pleurae; and there may also be observed fine interannular lines of brown pigment.

The ventral middle line is conspicuous in external view by its bright red colour, presumably due to the ventral blood-vessel showing through?.

The dorsal blood-vessel is less conspicuous in external view.

A colour-variation which I think is directly traceable to difference in habitat and nutrition is worthy of mention. The remarks already recorded as to the colour of the hepatic saccules referred to specimens obtained from the volcanic island of Matupi in Blanche Bay, New Britain. Those which I obtained from a small coral island (Pigeon Island) midway between Cape Gazelle and Blanche Bay had dark green liver-saccules.

<sup>&</sup>lt;sup>1</sup> This is not an appropriate designation, and I think it should be replaced by some such term as gonaducal line.

<sup>&</sup>lt;sup>2</sup> The blood of the Enteropneusta is an oxyphile non-corpusculated fluid, as shown by its intense affinity for eosin. Hence it seems probable that the red colour often observed in the region of the vascular trunks in living specimens is due to a substance like haemoglobin if not to haemoglobin itself.

#### PROBOSCIS.

In the anterior portion of the proboscis there is a small central cavity surrounded by a feeble aponeurosis. The cavity is not empty but contains a cellular conglomerate. Similar cell-débris have been observed by Spengel in the central cavity of the proboscis of *Pt. minuta* and elsewhere.

Farther back, but still in front of the central complex, the central cavity disappears<sup>1</sup>, its place being taken by the decussating and radiating bundles of connective tissue fibres. Immediately in front of the central complex the cavity again opens out, only to become nearly filled up once more by the extraordinarily abundant splanchnotheca in which the glomerulus (and central complex generally) is imbedded.

The anterior end of the glomerulus projects beyond the stomochord and pericardium but, in the main, the three principal components of the central complex are coextensive. The stomochord ends bluntly in front and does not taper as it does in *Pt. flava*. The pericardium ends simply, with no sign of bifurcation in front.

There is no well-defined lumen in the most anterior portion of the stomochord, but I will not undertake to deny its existence. The reason why I cannot speak certainly on this point in this case<sup>2</sup> is due to the fact that the cells of the stomochord are here inflated, more or less bladder-like, and decidedly more like chordatissue than I have seen in some other species.

The cavity of the **pericardium** is almost entirely filled by flocculent tissue resembling the splanchnotheca and containing minute granules, like the latter.

Dorso-ventral muscle-fibres accompany the central complex as usual.

The **central blood-space** attains enormous dimensions, far outstripping the subjacent stomochord. It is surrounded on all sides, except below, by a strong muscularis, derived, as usual, from the endothelium of the ventral wall of the pericardium, as is shown by the fact that no basement-membrane intervenes between the muscularis and the pericardial tissue.

The **ventral septum** is of less extent, both longitudinally and vertically, than in *Pt. flava*. It has a posterior free border, behind which the ventral canals fuse together to form a median tube, which dilates somewhat before terminating in the keel of the nuchal skeleton.

On nearing the nuchal region the musculature of the proboscis becomes more and more reduced in bulk, persisting for the longest distance in the ventral walls of the ventral canals. There is no circular thickening of the circular musculature at the base of the proboscis such as Spengel has described for *Pt. clavigera*, agreeing therefore in this respect with *Pt. aurantiaca*.

Accompanying the termination of the muscular fibres, the lateral walls of the dorsal canals and the dorsal walls of the ventral canals acquire a ciliated columnar epithelium. The right dorsal canal ends blindly in the feebly developed chondroid

<sup>&</sup>lt;sup>1</sup> This reduction of the coelomic cavity of the proboscis should be remembered in connection with the behaviour-of the proboscis-pore described below.

<sup>&</sup>lt;sup>2</sup> There is usually no doubt one way or the other. My material of the present species is quite faultlessly preserved.

tissue, while the left canal opens widely into a median end-vesicle terminating in an ill-defined pore which may open into the base of the medullary tube somewhat behind the anterior neuropore<sup>1</sup> (Pl. XXIX. Fig. 17 a—c). Behind the proboscis-pore, the ventral angles of the end-vesicle are continued for a short distance below the medullary tube as a pair of coecal pockets which may be separate or united. The association, here described, of the proboscis-pore and medullary tube, suggests morphological relationships of great significance and complexity of which I had previously no idea. The pore does not form a gaping orifice but is narrowed or even subdivided by a reduplication of the wall of the end-vesicle. The meaning of this reduplication will be apparent when we come to consider the West Indian species. In a younger specimen I find a simple undivided median end-vesicle opening to the exterior by a median pore in front of the anterior neuropore. The reduplication of the end-vesicle would therefore appear to be secondary in an ontogenetic sense—a fact of some interest.

#### STOMOCHORD.

The coecal dilatation of the stomochord is remarkable for the feeble development of the lateral pockets, and, connected therewith, its relatively small transverse expansion. The expansion in the dorso-ventral direction is approximately normal; in the transverse direction it is less than usual. There are both dorso-lateral and ventro-lateral subdivisions of the stomochordal lumen (Pl. XXIX. Fig. 17 a).

Tracing the stomochord in section from before backwards, its lumen is seen to be in a vestigial condition (reduced to zero or interrupted and broken) until near the posterior end of the coecal dilatation. Here the lumen widens out and the cells composing its dorsal wall are densely ciliated. This is an unexpected result, and the reason for the occurrence of cilia in this position is not very apparent, since the continuity of the stomochord is interrupted some distance in front of its buccal orifice.

Behind the coecal region the stomochord becomes abruptly reduced in bulk and continues to decrease in size until it reaches a point where it positively splits up into three minute portions separated from one another by processes from the dorsal edge of the nuchal skeleton (Pl. XXIX. Fig. 18). Finally these fragments of the stomochord unite with, and are absorbed into, the ventral wall of the wide terminal division of the stomochord, the dorsal wall of which is again finely ciliated. A similar, but more extensive fragmentation of the stomochord in the nuchal region, through its being traversed by bridges of skeletal substance is described by Spengel in Bal. kupfferi (Spengel, Mon., Taf. XV. Figs. 24—26).

### NUCHAL SKELETON.

The dorsal edges of the cupule of the nuchal skeleton are produced forwards as two thickened skeletal bands lying above the ventro-lateral pockets of the coecal dilatation of the stomochord (Pl. XXIX. Fig. 17 a). The body of the skeleton is produced dorsally into a high crest which is instrumental in effecting the fragmentation of the stomochord

<sup>&</sup>lt;sup>1</sup> Similar observations are recorded by Spengel in Bal. canadensis and Gl. talaboti. [Spengel, Mon. Taf. 17, Fig. 13, and Taf. 19, Fig. 6, page 607.]

described above. The alary processes are produced in front of the keel and bound the dorso-lateral sides of the ventral coecum of the proboscis-cavity, behind which they unite to form the keel. In the anterior region of the keel, the body of the skeleton is reduced to a thin flattened vertical band which becomes, for a short distance, absorbed into the substance of the keel, being almost entirely replaced by the latter. Farther back, the body again seems to assert itself, and the keel becomes reduced until the point of bifurcation is reached.

### COLLAR.

# COLLAR NERVE-CORD AND ROOTS.

At its anterior end the collar nerve-cord possesses a simple transverse lumen proceeding from the anterior neuropore. This soon ceases and the central canal is thereafter represented by a large number of separate minute medullary cavities, until the neighbourhood of the posterior neuropore is approached, when a large median lumen again occurs.

The first root is hollow throughout the greater part of its free course, but it is solid at its origin from the dorsal wall of the nerve-cord. It arises in front of the buccal orifice of the stomochord and has a long, oblique, forwardly directed course. The layer of peripheral nerve-fibres (Punktsubstanz) accompanying the root is relatively thick.

After fusing with the epidermis the lumen of the root, surrounded by an epithelial layer of cells, is continued for some distance forwards as an **intra-epidermal** canal lying within the thickness of the epidermis above the nervous layer. I have not observed this feature in any other species.

Immediately below the origin of the first root there is an indication of a small cavity in the nerve-cord, which however is quite filled up by a drop of deeply staining mucus like that which will be described below as occurring at the distal end of the vestigial root of *Spengelia porosa*.

The second root accompanies the anterior border of the dorsal septum of the collar. It is likewise hollow throughout its course, but solid at its origin and its central canal also runs for some distance  $(30-40 \,\mu)$  within the epidermis above the nervous layer. I do not think there is an actual opening to the exterior between the epidermal cells, but the latter are grouped round the distal end of this canalicular prolongation of the root in such a manner as to strongly suggest that at one time the root opened at the surface by a pore (Pl. XXIX. Fig. 19  $\alpha$  and 19 b).

The origin of the second root lies exactly at the level of the buccal orifice of the stomochord. Its course, like that of the first, is directed obliquely forwards.

In another specimen the first root is short and band-like, and its central canal vestigial, but the intra-epidermal canal into which it is produced in front possesses a continuous lumen and is remarkable for its great length—about 180  $\mu$ .

The second root is short, mostly solid and without intra-epidermal canal. A vestigial third root is present which is reduced at origin and insertion to little more

than a cylinder of basement-membrane; the cellular contents expand in the tract of the root which intervenes between the points of origin and insertion.

Finally, in the specimen now under consideration, the dorsal septum of the collar is lacking.

### COLLAR-CANALS AND PORES.

The collar-canals have a characteristically folded epithelium (Pl. XXX. Fig. 20). They open, on each side, into the first gill-pouch dorso-laterally with respect to the first gill-pore. It is a striking fact that the first gill-pore itself opens, together with the collar-pore, into the posterior end of the medullary tube immediately in front of the posterior neuropore, and in front of the posterior commissural ring-nerve of the collar (Pl. XXX. Fig. 21).

In another specimen these relations were not so striking, the opening of the first gill-slit occurring slightly farther back at the level of the posterior neuropore.

It is probably not a matter of very great importance whether the first gill-pore occurs a few thousandths of a millimetre in front of or behind the level of the posterior neuropore; and the same remark applies to the proboscis-pore in its relation to the anterior neuropore. What is perhaps of some importance is to take note of the fact that while the proboscis-pore may be intimately associated with the anterior neuropore, the collar-pores and first gill-pores may be similarly associated with the posterior neuropore.

## TRUNK.

#### BRANCHIAL REGION.

The genital pleurae become reduced in height as they approach the posterior rim of the collar, and they converge towards the middle line. The gonads do not extend to the anterior end of the genital pleurae but commence some distance behind the collar, as, indeed, is frequently the case (Spengel).

Spengel has shown that in those species in which the gill-clefts open into gill-pouches (i.e. in the majority of Enteropneusta) the gill-pouch is exactly as deep (dorso-ventrally) and as broad (longitudinally) as the corresponding gill-slit, except in Pt. gigas and Pt. clavigera, where the gill-pouches are produced ventrally below the base of the gill-slits into deep coecal diverticula. In Pt. carnosa such ventral coeca of the gill-pouches are also present and of great depth anteriorly, becoming shallower posteriorly (Pl. XXX. Fig. 22). At the posterior end of the branchial region the gill-pouches are very capacious in the transverse direction.

The tongue-bars are united to the corresponding septal bars by more than 30 synapticula on each side.

<sup>&</sup>lt;sup>1</sup> It might be said with equal justice and perhaps even with more accuracy that, in the specimen referred to, the posterior neuropore occurred at a slightly more anterior level.

## Branchiogenital Transition.

The external features of the branchiogenital transition are shown in Pl. XXVII. Fig. 6. The branchial tract assumes an elevated or vaulted form and the dorsal nerve-cord causes a crest-like projection.

The pharynx is succeeded by a thick-walled **postbranchial canal** similar in all essential respects to the corresponding structure in *Pt. flava* (Pl. XXX. Fig. 23). This structure has not previously been recorded in a member of the subgenus Tauroglossus. Its walls are formed of high, closely-packed, ciliated columnar cells, with nuclei at different levels, but especially crowded in the central portion of the epithelium. This postbranchial canal has a narrow lumen open continuously below into the main cavity of the gut. The last pair of gill-slits occurs at its dorsal borders as in *Pt. flava*. In front it constitutes a high median crest or duplication of the gut-wall which, posteriorly, becomes lower and lower until it disappears, and its place is then taken by an ordinary duplication of the gut-wall lined by normal gastral epithelium consisting of low, cubical, ciliated cells with basal nuclei.

The lateral septum arises on each side of the postbranchial canal behind which it arises from the dorso-lateral borders of the gut. In front of the postbranchial canal, that is, in front of the last gill-slit, both the origin and the insertion of the lateral septum occur in the basement-membrane of the epidermis. Its insertion marks the position of the gonaducal line which lies on the inner side of the genital pleura near the base, but separated by a wide interval from the branchial groove. Contrary however to what takes places in Pt. flava, the lateral septum only extends for a short distance into the branchial region and is by no means coextensive with the genital pleurae. In front of the lateral septum the gonaducal line is denoted by a fold of basement-membrane carrying a lateral blood-vessel; and moreover, this lateral blood-vessel occasions or is associated with the same interruption of the longitudinal musculature which accompanies the insertion of the lateral septum itself, Although, as mentioned above, the gonads do not, in this species, extend to the anterior end of the genital pleurae but commence two or three millimetres behind the posterior rim of the collar, nevertheless the gonaducal line, as defined by the presence of a lateral vessel and by the interruption of the longitudinal musculature, is continued beyond the anterior limit of the gonads to the anterior extremity of the genital pleurae.

Thus, although neither the gonads nor the lateral septa are coextensive anteriorly with the genital pleurae, the gonaducal line is. We have here, therefore, evidence of a recession of the gonads from the anterior end of the trunk.

In immature specimens the medial and lateral branches of the gonads, in the posterior branchial and genital region, abut simply upon the lateral or gonaducal line as shown in Fig. 23, Pl. XXX. In a mature female such as the one represented in Fig. 6, Pl. XXVI. accessory genital ducts occur laterally from the main series. It seems quite certain that the subdivision of the gonads which accompanies the appearance of accessory ducts, in *Pt. carnosa*, is simply due to growth and constriction from the original gonad; not to the formation of independent accessory gonads. There are no accessory ducts mediad of the gonaducal line, but the medial branches of the gonad

have become quite independent and their ducts occur a short distance removed from the line of insertion of the lateral septum. The mature gonads do not exhaust the entire capacity of the genital pleurae, but the distal free portion of the latter is left free from gonads. The eggs are quite small, as they are in all Ptychoderidae, and measure 15 mm. in diameter in the preserved state.

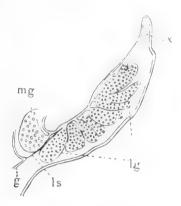


Fig. 2. Portion of transverse section through genital region of adult Pt. carnosa ?; showing lateral accessory genital ducts.

g. Gut-wall. lg. Lateral divisions of the gonad. ls. Lateral septum. mg. Medial branch of gonad with independent duct. x. Sterile border of pleural fold.

## GENITO-HEPATIC TRANSITION.

The most characteristic feature of this transition, namely, the abrupt termination of the genital pleurae (including the lateral septa), leaving a marked interval between them and the anterior hepatic saccules, has been already mentioned and is clearly shown in Fig. 6, Pl. XXVII.; this interval was even more pronounced in the living animal.

In this species therefore the gonads do not encroach upon the hepatic region. The wall of the gut in this region is thrown into a large number of folds arranged with some regularity. In the anterior portion of the hepatic region there are two specialised tracts of high, folded, ciliated epithelium, with basal nuclei and clear periphery, placed symmetrically at the ventro-lateral borders of the gut. Whether these remarkable tracts have any special significance I cannot say. I have not been able to find in this region any ciliated apparatus like that described above in Pt. flava. But I have (with difficulty owing to the extraordinarily folded wall of the gut) ascertained the existence of the two ptychoderoid ciliated intestinal grooves in the posterior hepatic and abdominal region.

## CAUDAL REGION; PYGOCHORD.

The abdominal and caudal regions of this species are extremely flaccid, and there is no external manifestation of the presence of a pygochord in the latter region. w. III.

Nevertheless, one is present. As shown in Pl. XXIX. Fig. 16, it is a very high, thin band with slightly dilated distal edge abutting upon the ventral vessel. It consists of ordinary cells as in Pt. flava. It probably does not possess great staying power in the present species. A pygochord seems to be of very general occurrence among the Ptychoderidae and affords a useful specific character.

### OECOLOGY.

Pt. carnosa burrows deeply in the sand and can draw itself along with astonishing rapidity. Its presence is betrayed by massive castings, which sometimes occur in such numbers as to form an important feature in the landscape at low tide. It lives at a depth of from one to two feet in the sand, both volcanic and coral, and may be taken anywhere between Cape Gazelle and the island of Matupi in Blanche Bay, New Britain. I first found it in Matupi.

In the same burrows another smaller species is to be found, namely, Pt. ruficollis n. sp. It breaks up into longer or shorter lengths upon slight provocation. I do not know whether or not fragments of the trunk would regenerate a head. There can be no doubt however as to the ability of the animal to regenerate its proboscis, which is often found more or less injured.

Often in the process of defecation the caudal end of the body is thrown off with the castings. An isolated piece, two or three inches long, of the abdominal region will always turn itself inside out.

The enormous size of the collar in this species, in some individuals more than in others, suggests that it not only assists the proboscis in the acts of burrowing and progression but even tends to supersede the proboscis. In other words, the collar of this species, and probably of some others, is more important than the proboscis as an essential organ of progression. This is therefore an indication of modification of function of the proboscis, and all such indications, however slight, should be carefully recorded.

# SUBGENUS 3. Ptychodera s. str.

# 3. Ptychodera ruficollis n. sp.

I was at first inclined to create a new subgenus for this well-marked species. When a Ptychodera has no genital pleurae, like Pt. hedleyi, the only obvious external character by which it can be recognised as a Ptychodera, is the presence of external hepatic saccules. The present species differs from all other Ptychoderidae, in the absence of these structures. This character, combined with the absence of pleural folds and with the small dimensions and triangular shape of the branchial tract<sup>1</sup>, renders this species as well-defined as could be wished. But it could hardly be identified as a Ptychodera from its external features alone, and I am still in some doubt as to the wisdom of not making a separate subgenus for it. Only two other Enteropneusta have been described with a triangular branchial tract, namely, Pt. minuta and Pt. sarniensis, from both of which Pt. ruficollis differs greatly.

## COLOUR, MEASUREMENTS AND EXTERNAL FORM.

Like other species of Enteropneusta the present form is characterised by a peculiarity in its colour. There is a strong crimson element in the collar which suggested the specific name. The colour of the proboscis in the living animal is light opaque yellow; that of the collar is dark reddish yellow, or yellow strongly tinged or shot with crimson. This combination of yellow and crimson gives the general effect of the colour known as Indian-red or Orange-red.

The crimson colour of the collar is chiefly confined to its anterior free portion and to the posterior region. The mid-region, which has the form of a circular cushion, seen in front of the broad dark-coloured groove in Fig. 7, Pl. XXVII., is generally without the crimson and is dark yellowish. The extreme posterior marginal band or so-called fifth zone of the collar is also free from crimson and is plain yellow.

The ground-colour of the trunk is a dull subtranslucent yellow except in the hepatic region, which is distinguished by a bright brown colour.

The proboscis is small and obtusely subconical in shape during life; it measures, in maximum extension beyond the rim of the collar, 4-4.5 mm.

The collar is much longer than the proboscis; its length is 6.5 to 7 mm., with maximum breadth in its hinder region of 5 mm. The branchial region is remarkable for its shortness, being sometimes even shorter than the collar; length 6—8 mm.

The genital ridges, whitish in colour, commence at the posterior end of the branchial region and extend back for some 50—60 mm., their maximum development occurring close behind the branchial region. The genital region is therefore many times longer than the branchial region—a good diagnostic feature. In Pt. hedleyi, with

<sup>1</sup> This is the "Kiemenfeld" of Spengel and "gill-area" of Hill.

which Pt. ruficollis seems to be more closely allied than with any other species, the genital region is less than half the length of the branchial region (Hill).

The hepatic region occupies approximately the third quarter of the body reckoned from the front. The rich brown colour which characterises this region is concentrated along parallel lines which run diagonally in two directions, decussating and so producing a striking lattice-work pattern. This condition could also be expressed by saying that the dermal annulations are broken up into diamond-shaped islets.

In the branchial region the dorsal vascular trunk is distinct and coloured red; otherwise the dorsal vessel is inconspicuous from outside. The ventral vessel on the contrary is very conspicuous with its deep red colour; it is bounded on each side by a longitudinal clear neutral-tinted area.

The general shape of the body is subcylindrical with a diameter of about 4 mm.

### PROBOSCIS.

The layer of circular muscles which lies next below the basement-membrane of the epidermis is thin, as is usual in Ptychodera, while the longitudinal muscles of the proboscis are arranged in radial bundles. The central cavity of the proboscis is not surrounded by a feltwork of conjunctive fibres.

### CENTRAL COMPLEX.

The anterior or distal extremity of the central complex of the proboscis in *Pt. ruficollis* differs greatly from the condition met with in the two species described above. The stomochord is not attenuated in front but terminates bluntly; the lumen extends practically to its distal end, and there is thus no solid prolongation.

The **pericardium** is bifid anteriorly, being produced forwards into two blind pouches, each of which is accompanied by the corresponding half of the glomerulus, for a short distance beyond the anterior limit of the stomochord (Pl. XXX. Fig. 24). This condition is comparable to what takes place in the Spengelidae, where, as was first described by Spengel in Schizocardium and Glandiceps, the pericardium is produced anteriorly into a pair of pericardial auricles (Herzohren).

The cavity of the pericardium is quite filled up by loose spongy tissue over a short stretch at its posterior end.

The **ventral septum** of the proboscis extends almost to the anterior extremity of the stomochord, its anterior free edge passing very obliquely downwards and backwards. It will be remembered that in *Pt. flava* the ventral septum ceases shortly in front of the dilated region of the stomochord, remote from the anterior end of the central complex.

At the front part of the coecal dilatation of the stomochord the lateral portions of the ventral coecum are seen to be projected forwards as paired lateral pouches (Pl. XXX. Fig. 25). It is clear that in many species of Enteropneusta the lateral pouches have to be considered equally with what Spengel has described as the ventral coecum only. In Pt. australiensis, Hill (loc. cit.) describes and figures the lateral

pouches of the stomochord. "From the transverse lumen of the blind sac," says Hill, "there passes forwards laterally a short horn on each side; a section passing through the proboscis neck just anterior to the passing down of the ventral blind sac lumen thus shows three cavities in the notochord," namely, two ventro-lateral and one dorso-median.

In *Pt. hedleyi* a similar condition has been described also by Hill. Here, in the region of the ventral blind sac the stomochord is transversely extended and "somewhat dorso-ventrally compressed. From the lumen of the blind sac there pass forwards two short lateral horns" as in *Pt. australiensis*.

In the mid-coecal region of the stomochord the latter has a characteristic helmet-shape in section, the ventro-lateral corners arching downwards over the ventral coelomic canals. In the median dorsal division of the helmet-shaped stomochord are numerous mucous gland-cells (Pl. XXX. Fig. 26).

Behind the coecal region, the character of the stomochord changes entirely. It is greatly reduced in bulk and its walls become thin and are apparently in a condition of mucous degeneration. In fact, the function of the stomochord as a supporting structure, a function which it undoubtedly serves in its anterior moiety, is, in the nuchal region, quite superseded by the nuchal skeleton.

The nuchal region of the stomochord is therefore in a retrograde condition, and we are prepared for the fragmentation described above in *Pt. carnosa* and by Spengel in *Bal. kupfferi*; and for the entire resorption of the nuchal portion of the stomochord which Spengel has described in old examples of *Sch. brasiliense* and in *Bal. canadensis*.

#### PROBOSCIS-PORE.

The dorsal proboscis-canals occur above the middle or coecal region of the stomochord, being separated from the ventral canals by the lateral pockets of the dilated stomochord and from each other by the dorsal wall of the pericardium, which meets the basement-membrane of the epidermis, as in other species (Pl. XXX. Fig. 25).

There is only one proboscis-pore, namely, that on the left side (Pl. XXX. Fig. 27). The left dorsal canal leads into an end-vesicle which lies in a median position above the pericardium, the apex of which is therefore shifted over to the right side.

The pore is coterminous with the end-vesicle, or, in other words, there is no coecal extension of the end-vesicle behind the pore. In different specimens there is great variation in the topographical relations of the various organs in the neck of the proboscis. Thus, in one case the left dorsal coelomic canal opens into the end-vesicle at the commencement of the coecal dilatation of the stomochord, *i.e.* at the commencement of the lateral pouches of the stomochord. The medianly placed end-vesicle accompanies the pouched region of the stomochord throughout its length, and opens by a sinistral pore at the transition from the coecal to the nuchal portion of the stomochord or, what is the same thing, at the transition from the cupule to the body of the nuchal skeleton; the pore therefore occurs well in front of the alary processes of the skeleton and in front of the posterior edge of the ventral septum, which, in this case, extends back into the free lobe described below.

In another specimen the left dorsal canal opens into the end-vesicle at the posterior end of the pouched or coecal region of the stomochord; the vesicle accompanies the body of the nuchal skeleton behind the cupule and opens by the sinistral pore at the level of the alary processes and posterior to the ventral septum which does not extend into the free lobe (Pl. XXX. Fig. 27).

In spite of these differences, however, the posterior border of the proboscis-pore is, in both cases, equally close to the insertion of the neck of the proboscis into the dorsal wall of the collar, and hence, equally near to the anterior neuropore.

Beyond the point of communication with the end-vesicle, the rest of the left canal breaks up into the islets of the chondroid tissue; and the right canal does the same. The **chondroid tissue** which was first described by Marion in 1885 and is called by Spengel the **secondary skeleton**, is one of the most remarkable elements in the organisation of these animals. In the present species it is poorly developed, as is usual for Ptychoderidae. It attains its maximum development in the Spengelidae. It needs little perspicacity to predict that when the theory of chondrification is better understood, the importance of this chondroid tissue in the Enteropneusta will be more fully appreciated.

The end-vesicle opens widely, like an exposed pit, as do the end-vesicles of Pt. flava. In Pt. hedleyi, Hill has shown that both sinistral and dextral pores are present, opening close together or by a common median aperture.

### VENTRAL COECUM OF PROBOSCIS.

The affinities which bind together the different species of Enteropneusta intertwine and overlap in the most perplexing manner. Thus, *Pt. ruficollis* differs from the other species of its subgenus and agrees with those of the subgenus *Chlamydothorax* in the mode of termination of the ventral coecum of the proboscis.

This coecal prolongation of the proboscis-coelom is continued far behind the posterior free edge of the ventral septum, and forms a large pro-eminent lobe which projects into the buccal cavity like the racemose organ of *Pt. flava* (Pl. XXVIII. Fig. 1 c, and Pl. XXX. Fig. 27). In *Pt. hedleyi*, the ventral coecum of the proboscis is stated by Hill to end blindly "in what appears to be simply the thickened basement-membrane of the epidermis" below the body of the nuchal skeleton.

In Pt. minuta it extends for a very short distance beyond the ventral septum as a flattened sac (Spengel, Mon., Taf. III. Fig. 30).

## NUCHAL SKELETON.

The anterior cupule of the nuchal skeleton in which the stomochordal coecum rests, presents no reliable features of diagnostic importance. The body of the skeleton following upon the cupule has, on the contrary, definite features characteristic of the species. It has a triradiate form closely resembling in outline the mitre-shaped stomochord which lies in front of it. It sits like a cap upon the ventral proboscis-canals

over which its lateral portions arch. The dorsal median portion projects into the base of the reduced stomochord, and may be described as cristate<sup>1</sup>.

Behind the level of the posterior edge of the ventral septum the body of the skeleton begins to alter its form. Its basal angles cease and their place is taken by the adventitious skeletal elements which constitute the alary processes (Pl. XXX. Fig. 27). Farther back these come together and unite to form the prominent keel which coexists in this species with the projecting lobe formed by the ventral coecum of the proboscis (Pl. XXX. Fig. 28).

#### COLLAR.

In respect of musculature and vascular system of the collar, the present species conforms to the Ptychoderoid type.

#### COLLAR NERVE-CORD AND ROOTS.

There is a continuous medullary canal in the collar nerve-cord of *Pt. ruficollis* which agrees therefore in this respect with *Pt. hedleyi* Hill. The dorsal wall of the neural canal is, as a rule, sharply delimited towards the lumen, while the inner surface of the ventral wall is sometimes quite irregular and without a clear line of demarcation. The central canal contains débris (Pl. XXX. Fig. 29).

Pt. ruficollis is remarkable for the large number of roots which may be present.

Series i. The first root (I) arises as a solid outgrowth from the dorsal wall very close behind the anterior neuropore; it is a slender root and has a winding course backwards at the anterior edge of the dorsal septum; it is doubtful whether this root contains any nerve-fibres, although it reaches up to the epidermis.

The second root (II) follows close upon the first and has also a long and winding course, but is much stouter than the first.

Root III arises at the level of the fusion of II with the epidermis. It runs horizontally backwards for a short distance, separated from the medullary cord by its own basement-membrane and by that of the cord itself, as well as by a thin layer of mesenchymatous tissue. As it proceeds backwards its calibre increases until finally it becomes connected for a second time with the wall of the medullary tube, and from this point it has a direct course to the epidermis. This remarkable condition would perhaps be more correctly expressed by saying that III does not approach the epidermis but runs backwards and fuses with IV. This at least is my interpretation of the matter. The fourth root, thus defined, is a broad sagittal band, not cylindrical.

After an interval, root V is given off; it has a direct, vertical course to the epidermis and is a normal cylindrical root, solid like the rest. Root VI resembles V in all respects. It is followed by another still longer interval, and then a stout root

<sup>&</sup>lt;sup>1</sup> Few of these statements are absolute. In one case the body of the nuchal skeleton between the cupule and the alary processes presents in outline an exact replica of the preceding triradiate stomochord as seen in section (Pl. XXX, Fig. 26). In another specimen the dorsal crest-like portion was barely represented, the dorsal side of the skeleton being concave with a very slight median crest.

(VII) unites the nerve-cord directly with the epidermis. VIII is band-like. IX is slender and arises a moderate distance behind VIII.

As the medullary tube nears the posterior portion of the collar-region it approaches the epidermis more and more, and the dorsal mesentery becomes progressively shorter. The consequence is that root X is very short and amounts to little more than a direct fusion of the nerve-tube with the epidermis. XI is quite slender and runs obliquely backwards, being followed by a twelfth root (XII) of similar character.

Series ii. The first root is band-like in its basal half and subcylindrical distally. It commences in front of the bifurcation of the nuchal skeleton, while its radical portion extends backwards in continuity with the nerve-cord beyond the bifurcation. It has a winding course in the dorsal septum shortly behind the free anterior margin of the latter.

The second root (II) has a band-like or crest-like origin; III is inclined forwards; IV has the vestige of an axial lumen at its base; V also has the vestige of an axial canal in continuity with the central canal of the medullary tube; VI has the merest trace of a basal diverticulum from the central canal; VII, VIII, and IX arise in close succession and are quite solid; a long interval occurs before X closely followed by XI is given off; XII has a horizontal course backwards, and is apparently without fibres.

About this region (i.e. in the hinder third of the cord) the central canal of the medullary tube has very irregular walls in the specimen under consideration. After another long interval a small root XIII occurs. XIV has interrupted vestiges of an axial lumen, but I could not trace this root continuously to the epidermis, and in fact I think it anastomoses with XV, which in its turn does not reach the epidermis but passes back to XVI which does. A much reduced root XVII occurs but does not reach the epidermis. There is a somewhat doubtful vestige of an eighteenth root which is immediately followed by the fusion of the nerve-cord and epidermis at the lip of the posterior neuropore.

#### COLLAR-CANALS AND PORES.

This species is particularly interesting in respect of its collar-canals in that it appears to afford a clue as to the origin of the dorsal plication which is such a frequent feature of the canals. In section this dorsal plication looks temptingly like a tongue-bar and the possibility of the collar-pores being modified gill-slits has been referred to by Morgan. It is therefore a matter of some importance to show conclusively that the dorsal plication is in no sense comparable to the tongue-bar of a gill-cleft. It is in fact simply due to the fusion of the infolded edges of the collar-funnel; a distinct raphe is discernible throughout almost the entire extent of the lappet.

The external aperture of the collar-canal, *i.e.* the collar-pore, opens as usual into the first gill-pouch. The dorsal plication projects beyond the limits of the collar-pore as a valve-like structure overhanging the branchial groove as far back as the second gill-pore (Pl. XXX. Fig. 30).

#### TRUNK.

### Branchial Region.

The character of this region is shown in Pl. XXVII. Fig. 7, and in section in Pl. XXX. Fig. 31.

The chief feature about it, namely, its shortness, has been already alluded to. Each half of a gill-cleft is crossed by 10—12 synapticula.

The **lateral septa** only extend for a short distance into the posterior portion of this region, namely, to the anterior border of the posterior depression of the branchial grooves, described below.

#### Branchiogenital transition.

At the posterior end of the branchial region, the branchial grooves undergo an abrupt and deep depression at the base of which the posterior gill-clefts open (Pl. XXVII. Fig. 7, and Pl. XXX. Fig. 32). A similar depression of the branchial grooves has been described by Hill in Pt. hedleyi. In Pt. ruficollis the depression is localised in the posterior end of the branchial region. In its deepest portion it bears a strong resemblance to the dermal pores which I have described in Spengelia porosa (see below, p. 275) into the base of the most anterior of which the posterior gill-slits likewise open.

At the posterior end of the branchial region the dorsal wall of the pharynx, i.e. the epibranchial ridge or band, sinks deeper below the surface and the height of the dorsal mesentery is correspondingly increased (Pl. XXX. Fig. 32). By this sinking inwards of the epibranchial ridge, the branchial division of the pharynx is reduced to zero, and the last pair of gill-pouches appear as small diverticula on each side of the epibranchial ridge, continuous with which a longitudinal ciliated groove passes back for some distance into the anterior portion of the genital region at the base of the postbranchial canal (Pl. XXX. Fig. 33).

The postbranchial canal of *Pt. ruficollis* differs greatly from the corresponding structure of *Pt. flava* and *Pt. carnosa*, both in its relations to the gill-slits and in its general character. In the two last-named species we have seen that the postbranchial canal is in direct continuity with the branchial portion of the gut, and that the terminal gill-clefts occur at its summit.

In Pt. ruficollis, on the contrary, the branchial division of the gut comes to an abrupt end, and the postbranchial canal appears as an independent diverticulum of the gut, while the terminal gill-clefts together with the longitudinal grooves continued behind them in the dorsal wall of the gut, lie at the base, instead of at the summit of the postbranchial canal. The relations here described are not only important in providing a clue as to the meaning of the postbranchial canal, but they are perhaps of even greater interest in furnishing a striking example of readjustment of topographical relations of gill-clefts.

The postbranchial canal of *Pt. ruficollis* projects forwards for some distance beyond the region of its communication with the gut, as a coecal tube, resembling, in this respect, the condition described by Hill in *Pt. hedleyi*. With regard to the latter species Hill says (*loc. cit.* p. 342):—"At its anterior end the dorsal diverticulum

projects forwards over the last pair of gill-pockets as a very short, free, blindly-ending tube."

Here the resemblance ends, for in Pt. ruficollis the walls of the diverticulum instead of being slightly folded as they are in Pt. hedleyi [Hill, l. c. Pl. XXII. Fig. 11], are thrown into the most complicated folds, so that the cavity is greatly subdivided and in section appears as a multiple lumen (Pl. XXX. Fig. 33). Its communication with the gut extends over a comparatively short distance, in fact there is little more than an elongated orifice of communication behind which it is again produced backwards, for a relatively long distance, as a coecal tube tapering slightly towards its posterior extremity. The lumen ceases some distance in front of its posterior end, and the structure is then a solid mass of densely nucleated tissue.

In mature specimens, the gonads actually penetrate into that portion of the perivisceral cavity which occurs between the attenuated free posterior end of the post-branchial canal and the dorsal wall of the gut.

The postbranchial canal of *Pt. ruficollis*, as here described, appears to me to present the characters of a **vestigial structure** for which I will at once proceed to offer an explanation, a certain amount of repetition being unavoidable.

# PT. FLAVA.

- 1. The pharynx varies greatly in length.
- 2. The postbranchial canal is the direct continuation of the branchial portion of the gut; it is neither produced anteriorly nor posteriorly as a coecal tube.
- 3. The terminal gill-clefts occur, and new ones arise in normal succession at the dorsal sides of the postbranchial canal.
- 4. The walls of the postbranchial canal are smooth, and its cavity is throughout in free communication with the ventral division of the gut.

### Pt. ruficollis.

- 1. The length of the branchial region is approximately constant, as shown by a dozen specimens; and it is characteristically short.
- 2. The postbranchial canal is not in direct continuity with the branchial portion of the gut; it is produced anteriorly and posteriorly, as a coecal tube, beyond the region of its communication with the cavity of the gut.
- 3. The terminal gill-clefts do not communicate with the postbranchial canal, but are quite separated from it, occurring in the dorsal wall of the ventral division of the gut below and beside the postbranchial canal.
- 4. The walls of the postbranchial canal are thrown into complex folds, by which its cavity is subdivided; it only communicates over a short stretch with the gut, and even then the orifice of communication may be interrupted; towards the posterior end of its free backwardly produced portion the lumen is obliterated, and replaced by a solid mass of tissue with densely packed nuclei.

My deduction from the foregoing data is, that the postbranchial canal represents what was formerly a greater posterior extension of the pharynx; that it is, in fact. the more or less metamorphosed relic of a portion of a primitively more extensive perforated pharynx. In Pt. flava, as well as in Pt. carnosa, it is still the seat of origin of new gill-clefts in the normal position. But in Pt. ruficollis, as well as in Pt. hedleyi, it is emancipated from any connection with the gill-clefts.

## GENITAL REGION.

In Pt. ruficollis there is a true genital region in a sense in which it is not present in Pt. flava. In the latter we saw that the gonads were emancipated from the main body of the animal. In the present species the gonads are incorporated into the body.

The species is remarkable for the great length of the postbranchial genital region, a peculiarity which it shares with Pt. sarniensis. There are no genital pleurae, but the dorso-lateral margins of the body are squared off sharply behind the branchial region and are continued backwards as longitudinal ridges between which the median dorsal region is sometimes depressed. But often the body is subcylindrical in shape, the prominence of the genital ridges no doubt depending upon the condition of the gonads and also upon the state of muscular contraction of the body.

The gonaducal lines (submedian lines of Spengel) in the genital region are seen in the living animal to be continuous with the branchial grooves.

The gonads encroach upon the branchial region, extending forwards (as shown in one series) to the level of the first gill-pouch on one side, and to that of the second gill-pouch on the other side. This difference of level of the anterior gonads is merely due to differences in the amount of their lobation, since the gonads of the first pair open approximately in the same plane between the fifth and sixth pairs of gill-pores.

The succession of the anterior seven genital ducts and their relation to the gill-pores is shown in the following table; a simple Roman numeral indicates that the genital duct occurs beside the corresponding gill-pore; two numerals connected by a hyphen indicates that the genital duct occurs between two gill-pores.

| lucts.   | Gill-pores. |  |           |  |  |  |  |
|----------|-------------|--|-----------|--|--|--|--|
|          | Right.      |  | Left.     |  |  |  |  |
| 1        | 1 1.1       |  | V VI.     |  |  |  |  |
| <u>·</u> | Z.111       |  | VI — VII. |  |  |  |  |
| 3        | XI          |  | VIII—IX.  |  |  |  |  |
| 4        | X           |  | X.        |  |  |  |  |
| 5        | ΧI          |  | XII.      |  |  |  |  |
| 6        | HIX IIX     |  | XIII.     |  |  |  |  |
| 7        | XIII        |  | XIV—XV.   |  |  |  |  |

The fact that the first pair of genital pores occurs between gill-pores V. and VI. again illustrates what I shall speak of later as the **recession of the gonads** from the anterior end of the trunk.

#### OVA.

I was fortunate in obtaining a quite mature female, whose gonads contained vast numbers of ripe ova. The eggs are enveloped in a stout vitelline membrane which closely hugs the unfertilised ovum. The ovum is round and small, and its contents are finely granular.

The germinal vesicle contains a large, usually marginal nucleolus, which has great attraction for eosin, and contains, one or many, fatty inclusions in its centre. In the unstained condition these refringent inclusions in the nucleolus are exceedingly prominent.

The diameter of these eggs is '09 mm., and this is a measurement of great importance because it is sufficient to inform us, I think with certainty, that the species (like all Ptychoderidae) develops indirectly through a Tornaria-stage.

The mode of oviposition of the Enteropneusta does not seem to be perfectly understood [cf. Spengel, Mon., p. 658], and observations which I have made on Pt. ruficollis are therefore of interest. Although the gonads are connected to the skin by so-called ducts, Bateson thought that the eggs were discharged by rupture of the body-wall as they are in many Annelids. As shown in Plate XXXII. Fig. 69, at the time when the ova are ready to be discharged the genital duct, in this species, becomes properly hollowed out, and gapes widely enough for the passage of the ova without any squeezing.

#### GENITO-HEPATIC TRANSITION.

Sometimes the genital ridges can be traced for some distance into the hepatic region; sometimes they stop short some distance in front of the hepatic region. The noteworthy point about the transition internally, is the occurrence of a longitudinal ciliated tract on the left side about midway between the dorso-lateral margin of the body and the ventral nerve-cord. This ciliated band is partly overhung by a fold of intestinal epithelium, and appears to be comparable to the ciliated apparatus in the gut of other Ptychoderidae.

I was not able to ascertain how far this band extended into the abdominal region. The post-genital portion of the body of this species is almost impossible to preserve intact as the body-wall is very thin and brittle. Only the caudal region always preserves its integrity.

The wall of the gut in the hepatic region is thrown into numerous sacculations throughout its entire circumference. These do not normally produce lobes of the bodywall which would be visible externally.

<sup>1</sup> Possibly the discharge of the large eggs in the Balanoglossidae may be accompanied by rupture.

#### ABDOMINAL-CAUDAL TRANSITION.

The ventral nerve-cord in the abdominal region lies at the base of a groove which comes to an abrupt termination at the junction of the abdominal and caudal regions (Pl. XXVII. Fig. 7).

The surface of the body in the caudal region is smoother than in the abdominal region, and the dermal annulations more regular.

The body-wall in the abdominal region is flaccid and highly collapsible, while the caudal region is always well distended. The rigidity of the caudal region is no doubt partly due to the circular musculature, and partly to the presence of a stout **pygo-chord** (Pl. XXX. Fig. 35). The ventral dilated edge of the pygochord consists of a cord of large cells, each with a central nucleus from whose neighbourhood radiating strands of protoplasm pass to the periphery of the cell, strongly reminding the observer of the axial cells of the tentacle of a Campanularian hydroid. Similar cells with stellate contents occur in the superjacent constrictions of the pygochord.

# MUSCULATURE OF BODY-WALL.

Pt. ruficollis agrees with Pt. hedleyi Hill in the absence of circular muscles from the body-wall of the trunk except in the caudal region. At the anal extremity they combine with the muscularis of the gut-wall to form a sphincter ani.

## OECOLOGY.

Pt. ruficollis lives commensally with Pt. carnosa in so far that it inhabits the burrows of the latter. At the volcanic island of Matupi in Blanche Bay (New Britain) when one investigates the Enteropneustic castings with the aid of a spade it is almost an even chance whether one will unearth the one species or the other, although Pt. carnosa is the predominant form. At the coral islet known to the local whites as Pigeon Island and to the native blacks as Palakuvur Pt. ruficollis is the predominant form or at least it is the one which is easier to procure.

Both these species are victims of autotomy; but whereas Pt. carnosa is thick and fleshy, Pt. ruficollis is thin and brittle.

# FAMILY. SPENGELIDAE.

#### GENUS. SPENGELIA.

4. Spengelia porosa Willey.

A. Willey. Spengelia; a new Genus of Enteropneusta. Q. J. M. S. Vol. xl. 1898, p. 623.

# COLOUR, MEASUREMENTS AND EXTERNAL FORM.

Proboscis, rich yellow; collar, bright orange; body, dull yellow. The distinctive feature in regard to the colour of this species is the bright orange of the collar.

The length of the proboscis, in the fresh condition, greatly exceeds that of the collar. During extension it measured up to 10.5 mm. in length; the collar under the same conditions measured 6.25 mm. After preservation the proboscis contracted to 5.25 mm, and the collar to 4 mm.

The general shape of the body is subcylindrical and the body-wall is stout and firm.

In the branchial region the body is quite cylindrical and faintly annulated. The diameter of the body, in this region, alike in the vertical and transverse directions, measures 5 mm. The gill-area, *i.e.*, the dorsal tract bounded by the branchial grooves, is long and band-like, measuring, in the living animal 30 mm. in length. The gill-pores are visible externally in each branchial groove (Pl. XXVII. Fig. 8).

Only twenty millimetres of the postbranchial genital region were present in the single available specimen, the posterior half of the body being lost.

The genital region is characterised on its dorsal side by the presence of a double series of very extraordinary dermal pits which dip down into the body for a relatively great depth. They may be defined as special intergonadial depressions of the interannular grooves of the body-wall. The mouth of each pit measures about 1 mm. in diameter, and the pits taper towards their internal extremities which, except in the case of the most anterior pits, end blindly near the wall of the gut (Text-fig. 3).

## PROBOSCIS.

All that need be noted here about the musculature of the proboscis is that the longitudinal muscles are not disposed in radial bundles as they are in the Ptychoderidae, and that the circular muscles are strongly developed.

# VERMIFORM PROCESS OF STOMOCHORD.

The stomochord is produced in front into a long vermiform process like that described by Spengel in Schizocardium and Glandiceps. This process consists of a generally solid cord of undifferentiated cells lying in the median septum of the proboscis. It is coextensive with the median septum extending with the latter through about one-third of the length of the proboscis (Pl. XXXI. Fig. 36, and Pl. XXVII. Fig. 8 A). In front of the median septum the central cavity of the proboscis is an undivided well-defined space.

The vermiform process is surrounded by a stout basement-membrane but is of unequal calibre. It serves, in great part, for the insertion of the median dorso-ventral muscles of the proboscis; but often the muscular fibres pass across the centrum of the proboscis apparently without being inserted into the basement-membrane of the vermiform process.

The economic importance of the vermiform process appears to lie in its capacity for producing basement-membrane.

The dorso-ventral muscles are quite distinct in the median septum itself; but outside the latter the fibres soon appear to alter their course and are lost in the general longitudinal musculature. On the dorsal side of the median septum the fibres may be observed to pass through the aponeurosis formed by the closely felted connective-tissue fibres which surround the central cavity of the proboscis. This aponeurosis is interrupted at intervals along the ventral edge of the median septum and is never so strongly developed ventrally as dorsally (Pl. XXXI. Fig. 36).

On issuing from the median septum, the dorso-ventral muscles form, both dorsally and ventrally, two divergent bundles; and it is these bundles which farther back, bound the lateral surfaces of the dorsal<sup>1</sup> and ventral septa of the proboscis.

At some points the vermiform process may be reduced to the basement-membrane which surrounds the axial cord of cells, no cell-elements being visible at such places.

At the bifurcation of the ventral bundles of the dorso-ventral muscles, there is a longitudinal blood-vessel which rises from the basement-membrane of the ventral epidermis about at the level of the anterior end of the vermiform process. This vessel arches upwards from its point of origin until it reaches the position just described when it runs backwards parallel with the vermiform process. It probably connects the ventral dermal vessels of the proboscis with the central blood-space although I was not able to trace its actual connection with the latter. In accordance with Spengel's nomenclature it is to be defined as the ventral **recurrent dermal vessel** of S. porosa and the characteristic feature is that it occurs entirely in front of and independent of the ventral septum of the proboscis<sup>2</sup>. The afferent dermal vessel, as in other Enteropneusta [Spengel, Mon., p. 81], occurs dorsally much farther back near the posterior end of the pericardium approximately at the junction of the dorsal truncal vessel with the central blood-space, i.e. in the nuchal region.

The aponeurosis round the central cavity of the proboscis dwindles out posteriorly in front of the glomerular region.

 $<sup>^{1}</sup>$  The dorsal septum of the proboscis, as already mentioned, is formed by the dorso-lateral wall of the pericardium.

<sup>&</sup>lt;sup>2</sup> The dermal vessels of the proboscis are much clearer in the species next to be described, Spengelia alba.

#### CENTRAL COMPLEX.

The pericardium is bifurcated in front and the right and left halves of the glomerulus are likewise produced for a short distance in front of the body of the stomochord, but the pericardial auricles (Herzohren) are not long, definite structures as described by Spengel in Schizocardium but moderately developed (Pl. XXXI. Fig. 37). Of the two anterior horns into which the glomerulus is produced the left is larger and longer than the right in my preparations, and in correspondence with this condition the right pericardial auricle is feebly developed, the bulk of the pericardium and central blood-space passing over to the left division of the glomerulus. The left auricle can be traced through about half the course of the left horn of the glomerulus.

The ventral septum of the proboscis commences at the junction of the vermiform process with the body of the stomochord. The latter is somewhat flattened transversely in front and contains a multiple, interrupted lumen. In addition to the usual elongated fibre-like interlacing cellular tissue, there are numerous deeply staining gland-cells in the neighbourhood of the lumen. At some points the lumen is reduced to the merest trace and the stomochord is then, to all intents and purposes, solid.

The cavity of the pericardium contains a mass of loose cellular tissue chiefly derived by proliferation from the ventral wall. The dorsal wall of the pericardium is flat in front but soon becomes elevated into a hollow crest which meets and fuses with the basement-membrane of the epidermis shortly in front of the coecal region of the stomochord.

The character of the stomochord changes in the vicinity of the coecal dilatation. Its dorsal wall becomes elevated into a broad, rounded crest which projects into the ventral wall of the pericardium. The lumen widens out in the centre of the dorsal crest and gives off a median ventral diverticulum which forms the cavity of the thickened ventral half of the stomochord. The cavity of this so-called **ventral coecum** soon loses its integrity and is represented by numerous small disconnected cavities which occur between the lateral pouches of the stomochord.

The lateral pouches of the stomochord are very distinct structures. Each contains a spacious cavity lined by well-defined columnar epithelium (except mesially where the cavity is bounded by the body of the stomochord). The pouches tend to project forwards for a short distance as coecal pockets lying in a sheath of chondroid tissue. In their middle portion the lateral pouches are separated by the sub-solid body of the stomochord; but more posteriorly their cavities communicate transversely, thus forming the posterior portion of the ventral coecum which projects backwards into the cupule of the nuchal skeleton (cf. Pl. XXXI. Fig. 38).

## NUCHAL SKELETON.

The ventral proboscis-canals come to an end posteriorly in the chondroid tissue, without fusing together. This is another of the many points in which Spengelia shows relationship to Glandiceps. By their ending in this manner they make way for the enormous keel of the nuchal skeleton. Thus their behaviour in this species is the exact converse of what has been described above for Pt. flava. The large keel and

the intimate relation between the substance of the nuchal skeleton and the chondroid tissue, are the salient features in the nuchal skeleton of this species (Pl. XXXI. Fig. 39). The cornua of the skeleton, as already mentioned in the classification, extend to the posterior region of the collar (Pl. XXVIII. Fig. 1 d). The keel diminishes posteriorly, ceasing entirely some distance in front of the point of bifurcation; the body of the skeleton has then (i.e. behind the keel) a cubical shape with rounded edges.

## PROBOSCIS-PORE.

The right dorsal canal ends blindly, while the left communicates with an end-vesicle which opens to the exterior by a narrow pore on the left side (Pl. XXXI. Fig. 39). The pore is very long, slit-like and approximately co-terminous with the end-vesicle; in both of which features the present species differs from S. alba. The right canal has a narrow dorsal canalicular extension corresponding to the place where it would communicate with an end-vesicle, were one present on that side. In the vicinity of the point of communication between the left canal and its end-vesicle, there are muscular fibres about the base of the vesicle which appear as if they would act as a sphincter.

# COLLAR.

## COLLAR NERVE-CORD.

The medulla of *Spengelia porosa* does not contain a continuous central canal but a large number of small disconnected medullary cavities arranged quite irregularly (Pl. XXXI. Fig. 41).

The anterior neuropore leads into a broad, transverse, median lumen which soon gives place to a series of lateral cavities at each side of the nerve-cord. In addition to these lateral cavities there are other smaller cavities scattered about in the substance of the cord. Here and there cavities seem to be entirely absent and the cord at such places appears quite solid in section.

In the neighbourhood of the medullary cavities there occur numbers of deeply staining mucous cells, not unlike those found in a similar position in relation to the fragmented lumen of the stomochord.

The nerve-fibre layer is confined to the ventral side and to the lateral margins of the cord, but is absent from the median dorsal tract.

The collar cord of the present species is remarkable for the presence of at least one **vestigial root**. It is no new thing for a root not to reach the epidermis but it is new for it to behave as it does in S. porosa (Pl. XXXI. Figs. 40 a—40 c).

The vestigial root which claims special attention occurs in the region of the bifurcation of the nuchal skeleton. It arises from the non-fibrous dorsal side of the cord slightly to the right of the middle line. It bends first to the right and then runs forward for an appreciable distance, without however reaching the basement-membrane of the epidermis. On the contrary, it abuts upon and terminates in a relatively dilated vesicle, the walls of which are crowded with some mucoid substance

which stains black with haematoxylin. The end-vesicle of this vestigial root would in fact seem to be in a condition of mucoid degeneration. The root itself contains a well-marked, though interrupted vestige of an axial canal, which however does not communicate with any of the medullary cavities of the cord, although immediately behind and at the base of the root there occurs a comparatively large medullary cavity.

The posterior portion of the collar nerve-cord, like the anterior, contains a broad continuous lumen and it is at the commencement of this posterior lumen that a low hollow pouch-like diverticulum arises to the right of the middle line. It is quite short and does not appear in section separate from the nerve-cord. It is open to anyone to regard this structure as a second vestigial root, to which, however, no special interest attaches.

### PERIPHARYNGEAL CAVITIES.

In my preliminary diagnosis of this species I stated that there were no peripharyngeal cavities. Having since been so fortunate as to obtain a second species of the genus, my examination of it led me to re-investigate S. porosa in respect of this quality and I find that there is a pair of peripharyngeal cavities in a vestigial condition.

Their vestigial nature is clearly established by the fact that they are closed behind as well as in front and therefore do not communicate with the body-cavity of the trunk.

In Schizocardium, Spengel has shown that the right and left peripharyngeal spaces are triangular in shape, the apex of the triangle being directed forwards and reaching to the level of the point of bifurcation of the nuchal skeleton; the base of the triangle lies at the posterior end of the collar where the cavity enters into free communication with the truncal coelom.

This condition is indeed met with in Spengelia alba n. sp. In the present species, however, the peripharyngeal cavities are pointed at both ends, sharply pointed in front and bluntly behind. The anterior extremity reaches to a point shortly behind the level of the bifurcation of the nuchal skeleton. As the cornua of the latter divaricate, the dorso-ventral extension of the peripharyngeal cavity (on each side) increases, until a maximum is reached in the mid-region of the collar. Then reduction commences; the dorsal edge of the cavity, which is always separated by an interval from the edge of the perihaemal cavity of its side, recedes further and further from the vicinity of the latter, the ventral extension of the cavity becomes likewise reduced until the entire cavity ceases some distance in front of the termination of the nuchal skeleton. The posterior end of the cavity lies against the throat-epithelium half-way between the dorsal and ventral sides of the latter (Pl. XXXI. Fig. 44).

#### COLLAR-COELOM AND PORES.

There is no dorsal septum in the collar, except the fold of basement-membrane associated with the first vestigial root, which is probably to be regarded as a vestige of the dorsal septum. On the other hand, the ventral septum has an unusual forward

extension, commencing a short distance behind the region of bifurcation of the nuchal skeleton; it is a much folded membrane containing blood-spaces.

The collar-canals have the usual semilunar funnel opening into the posterior dorsal portion of the collar cavity. The ciliated columnar epithelium of the canals has a striated inner portion free from nuclei, and a basal two-thirds, with densely crowded nuclei which stain nearly black with ordinary haematoxylin. The dorsal wall of the canals is lightly plicated, but there is no definite tongue-like fold such as occurs in many other species (Pl. XXXI. Fig. 42).

## PERIHAEMAL CAVITIES AND CANALS.

The perihaemal cavities, as is known, are prolongations from the truncal coelom into the collar. In Spengelia, as in all Enteropneusta except the Ptychoderidae, they contain transverse muscles below the longitudinal muscles. Their most noteworthy feature in S. porosa, however, is due to the presence of a pair of canals, analogous to the collar canals, which open like the latter, into the first pair of gill-pouches from which they are derived (Pl. XXXI. Fig. 44). These structures also occur in S. alba, n. sp. In the present species they lie imbedded in the spongy connective-tissue which is abundant in the posterior region of the perihaemal cavities. They are long canals, and perfectly definite, and I knew of their existence long before realising their probable significance. Their epithelium is of a spongy nature, and contains mucous cells. The lumen is to a large extent occluded in my preparations, so that it is not possible to assert positively that these canals open into the perihaemal cavities. The latter are cavities only in name, being filled up by muscular and connective tissue, so that there could hardly be an effective opening into the cavities. Nevertheless in the following species which I have to describe, the conditions are more favourable for observation, and there is more reason to suspect the existence of an internal pore in that case.

In the present species, at least in the adult, my impression is that these structures are not of great functional importance, they are in fact vestiges of a former condition of which we know nothing definitely. I regard them as **truncal pores** homodynamous with the collar pores and the proboscis pores, and the true homologues of the atrio-coelomic funnels (brown funnels) described by Lankester in Amphioxus. These latter structures have fallen into desuetude phyletically, since the evolution, and historically since Boveri's discovery, of the nephric tubules<sup>1</sup>.

### SPLANCHNIC LAYER OF NERVE-FIBRES.

There is a well-defined layer of "Punktsubstanz" at the base of the throat epithelium. It is thicker in front than behind. It also occurs at the base of the epithelium of the esophageal portion of the pharynx.

Spengel has also described such "Punktsubstanz" in places where one might not have expected to find it. I have seen it at the base of the branchial epithelium of the septal bars in Pt. flava.

<sup>&</sup>lt;sup>1</sup> For further remarks, see below p. 310 et seq.

#### TRUNK.

### BRANCHIAL REGION.

The present species is characterised by the presence of a paired series of medial gonads, mediad of the branchial grooves, in addition to the main lateral series (Pl. XXXI. Fig. 45).

This is a feature which it possesses in common with the genus *Glandiceps*; while the fact that the branchial bars are united together by synapticula or crossbars (of which there are about ten in a vertical row) removes it from *Glandiceps* and approximates it to *Schizocardium* and the Ptychoderidae.

It is a fact of topographical interest which is exhibited in horizontal sections through the pharynx—such sections cutting the gill-bars transversely—that whereas in the entire genus *Ptychodera*, the tongue-bars project into the cavity of the pharynx beyond the septal bars, in *Spengelia* these relations are reversed, the septal bars projecting into the pharynx beyond the tongue-bars. In other Enteropneusta the conditions appear, judging from Spengel's figures, to differ according to the species.

The lateral gonads appear in section at the level of the first gill-pore, but the first genital duct occurs at the level of the fourth gill-pore; the medial gonads commence at the level of the fourth gill-pore. The genital ducts of the lateral series open at the outer sides of the branchial grooves, while those of the medial series open at the inner sides of the grooves. Apart from the medial genital ducts there are no accessory ducts in the branchial region. Mediad of the lateral ducts may be found a lateral (genital) blood-vessel.

The gut in the branchial region is provided with a well-developed lower cesophageal portion in the form of a deep groove, and the parabranchial ridges are nearly as definitely demarcated as in the Ptychoderidae.

The circular musculature of the body-wall is internal to the longitudinal musculature, instead of being external as it is in the Ptychoderidae; it agrees in its disposition with that described by Spengel in *Glandiceps*, namely, the fibres arise at the peripheral margins of the dorsal and ventral septa, and pass between the dorsal and ventral sides of the body applied to the inner surface of the longitudinal musculature, the muscularis of the gut being independent of the dermal musculature. In *Schizocardium*, Spengel has shown that the muscularis of the gut, at least in the branchial region, is derived from the dermal musculature.

## GENITAL REGION.

This region is characterised on the dorsal side by a right and left series of very remarkable dermal pits which dip deep down between the gonads and actually penetrate to some degree amongst them. They probably serve for the irrigation of the gonads, as suggested in my preliminary account of this species, and in this capacity are to be compared physiologically with the subgenital pits of Discomedusae, and the funnel-like depressions of Lucernariidae.

The dermal pits of this species are so deep that they extend through more than half the thickness of the body as shown in Text-figure 3. They lie in the

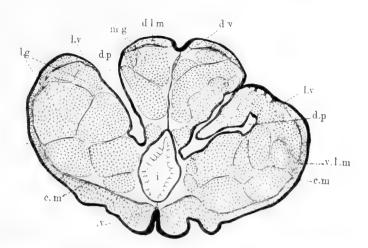


Fig. 3. Transverse section through genital region of Spengelia porosa showing dermal pits and pores.

On the left of the figure a dermal pit is cut through the middle of its external orifice; on the right it is cut tangentially.

c.m. Circular muscles. d.l.m. Dorsal longitudinal muscles. d.p. Dermal pits. d.v. Dorsal vessel. l.g. Lateral gonads (accessory genital ducts shown on the right). l.v. Lateral vessel. m.g. Medial gonads. v. Ventral vessel. v.l.m. Ventro-lateral longitudinal muscles.

submedian line, in direct continuation from the branchial groove on each side. They are roughly but not exactly paired, no more than are the gill-clefts themselves. The mouth of each pit is about 1 mm. in diameter. The most anterior pits invade the posterior extremity of the branchial region, in consequence of which a number of the outer pores of the posterior gill-slits do not open near the surface of the body, but deep down at the base of the dermal pits. Apart from their connection with the gut by means of the posterior gill-slits, the dermal pits do not communicate with the intestine, although they extend very near to the wall of the latter.

In the fresh condition the sides of the genital region were occupied by elongated, somewhat pyriform bodies, which caused definite ridges on the external surface. These projections were caused by the gonads.

In the genital region accessory genital ducts occur both laterally and medially from the dermal pits, so that several may be met with in a single transverse section. The accessory pores of the lateral gonads do not perforate the longitudinal musculature, but all occur within the interval, which is a very wide one, between the dorsal longitudinal musculature, and the upper margin of the ventro-lateral longitudinal muscles (Text-figure 3).

The post-genital portion of the body was lacking from the single specimen which was available for microscope examination. The individual was a mature male.

### OECOLOGY.

I found this species in company with *Pt. flava* in rock-pools, which contained sand between the tide-marks on the weather side of Lifu. I had two specimens, only one of which was available for cutting into sections, the other was overlooked until my arrival home, when it was found to be macerated, but not useless (see Pl XXVII. Fig. 8 a and Pl. XXVIII. Fig. 1d).

My former account of Sp. porosa (loc. cit.) was illustrated by a sketch drawn from the living animal which showed the dermal pits in the genital region in dorsal view. These pits introduce us to a new category of structures in the Enteropneusta.

Besides the truncal canals of *Spengelia* there is another ancient structure which occurs in the Spengelidae and nowhere else among the Enteropneusta. I refer to the vermiform process of the stomochord. Apart from what is stated near the end of this memoir I shall not attempt to offer an explanation of this organ, although I believe one is possible. Suffice it to say that, for my part, I am convinced that the vermiform process is to be regarded as an integral constituent of the stomochordal complex, but that it has only been retained by the members of this family. As I have just intimated, I think it is possible to arrive at the probable approximate explanation of the vermiform process, but it would be difficult, at present, to make it convincing.

## 5. Spengelia alba n. sp.

## COLOUR, MEASUREMENTS AND EXTERNAL FORM.

This species is remarkable on account of its almost uniformly dull white colour. During life the proboscis and collar were opaque white; the anterior free portion of the collar was plain white, and was followed by a watery white zone; then came a white ridge, followed by another watery white zone, which was separated by the usual circular groove from the posterior white band of the collar. In the hepatic region there were green and brown tints.

The proboscis when extended attained a length of 10—11 mm. (after preservation 8 mm.), and was cylindrical in shape. The collar under the same conditions attained a maximum length of 6.5 mm. (after preservation 4 mm.).

Behind the branchial region the trunk appeared to have a ventral curvature impressed upon it, and the ventral side of the body in the hepatic and abdominal regions was distinctly carinate, the median tract being marked off, on each side, by a deep longitudinal groove, from the rest of the body (Pl. XXVII. Fig. 9).

The branchial region, 18 mm. in length, is characterised by the elongated, even, band-like gill-area. The body in this region has a transverse diameter of 3.5 mm., and a vertical diameter of 4.5 mm. The entire body of the animal may be described as long and slender.

The genital region, 25.5 mm. in length, is characterised externally by the presence of dermal pits which are very similar in superficial appearance to the corresponding structures in S. porosa; but in section they are found to be much shallower.

The hepatic region, characterised by its green and brown coloration, had according to my notes a length of 14—15 mm. The effect of preservation was to cause this region to lengthen rather than to contract and in the preserved condition I should put the length of it as nearer 20 mm. There are no external liver saccules although, when fresh, the annular ridges were found to be turgid and to present the appearance of rudimentary saccules, an appearance which was almost entirely lost after preservation. Nevertheless even in the spirit specimen some of the dorsal annular ridges of the anterior portion of the hepatic region tend to be more pronounced than the ordinary ridges.

The hepatic region is above all characterised by the presence on each side of the body of a smooth glandless epidermal tract lying nearer to the ventral than to the dorsal side of the body. It commences in front, at the posterior end of the genital region as a wide area quickly narrowing down to a narrow streak, which widens out again to a breadth of about 1.25 mm. in the mid-hepatic region. From the region of maximum breadth it gradually narrows down posteriorly and is continued for some distance into the abdominal region (Pl. XXVII. Figs. 9 B and 9 c).

In the fresh state I observed brown loculi showing through this ventro-lateral tract in its wide portion, due presumably to the local turgidity of the gastral wall.

There is no such glandless tract over the greater part of the abdominal region (60 mm. in length), but its place is taken on each side by a shallow groove which is not associated with absence of glandular ridges. The effect of these grooves is to raise the median ventral tract into a prominent rounded keel. The caudal region (about 14 mm.) is slightly swollen and is only distinguished externally by the flattening out of the above-described grooves and the consequent absence of a ventral keel.

### PROBOSCIS.

The central cavity is sharply defined and extends nearly to the tip of the proboscis. Anteriorly it is surrounded by a uniform layer of felted fibres and it is difficult to distinguish the dorsal and ventral sides of the cavity. Farther back the decussation of the fibres denotes the dorsal side. But from the extreme front end of the proboscis the ventral middle line is defined by the presence of the ventral recurrent vessel which lies immediately inside the layer of circular muscles and communicates at frequent intervals with the epidermal system of blood-vessels (i.e. the blood-spaces in the basement-membrane of the epidermis) by perforating the circular musculature. A similar recurrent vessel is present in S. porosa, where it rises up to a more dorsal position below the vermiform process. In the present species the recurrent vessel retains its ventral position adjacent to the circular musculature until it passes up along the free edge of the ventral septum (Pl. XXXI. Figs. 46—47).

The dorsal recurrent dermal vessel runs, as is its wont, along the anterior edge of the pericardium in front of which its distal portion forms a vascular complex. (Pl. XXXI. Fig. 47).

The circular musculature of the proboscis is generally thicker than the nervous layer of the epidermis.

The vermiform process of the stomochord is of varying calibre and in its anterior portion there is, in one or two places, an actual discontinuity, as if a certain amount of fragmentation had taken place. It is solid and its cells are undifferentiated in the anterior two-thirds, becoming vacuolar as the body of the stomochord is approached. The vermiform process is supported in the thin median septum of the proboscis, and the dorso-ventral muscles are inserted into the basement-membrane surrounding it (Pl. XXXI. Fig. 46). The vermiform process passes quite gradually into the body of the stomochord and it is impossible to say where one begins and the other ends.

The pericardial auricles are very minute, almost non-existent, but the glomerulus projects beyond the anterior limit of the pericardium for a moderate distance as paired glomerular horns at the sides of the stomochord.

The **ventral septum** has a forwardly directed free edge and does not extend to the base of the vermiform process or to what might be considered as such but falls somewhat behind the anterior region of the main body of the stomochord.

In the coecal region of the stomochord the **lateral pouches** are extremely well-marked and tend to project slightly forwards as independent pouches. Unlike S. porosa, their cavities do not communicate across the middle line but remain separate until

they die out (Pl. XXXI. Fig. 48). Other minute cavities or vestiges occur in the body of the dilated stomochord in addition to the main lumen, which is also interrupted.

The **ventral canals** terminate in the chondroid tissue without communicating with each other, as in *Glandiceps*.

Of the dorsal canals only the left communicates with an end-vesicle which is sinistral in position (not quite median) and opens by a short narrow sinistral pore to the exterior (Pl. XXXI. Fig. 49). Behind the **proboscis-pore** the basement-membrane surrounding the vesicle closes in once more and the end-vesicle is continued for a relatively long distance (about  $100 \mu$ ) as a coecal tube, the posterior end of which actually projects into the anterior end of the left perihaemal cavity<sup>1</sup> (Pl. XXXI. Fig. 50).

The prae-trematic, post-trematic and trematic behaviour of the end-vesicle of the proboscis canals is of the very greatest importance to anyone willing to penetrate into the morphological tangle surrounding these structures. The post-trematic prolongation of the end-vesicle of S. alba is therefore worthy of particular note as being one of the most striking characters of the species.

The **nuchal skeleton** resembles that of *S. porosa* in the main. Its principal characters are sufficiently shown in the figures to obviate a detailed verbal description (Pl. XXXI. Figs. 49—51).

### COLLAR.

Not only is the collar musculature (inner longitudinal muscles and perihaemal muscles) projected into the neck of the proboscis but the **anterior neuropore** also occurs at the posterior end of the nuchal region and is independent of the duplicature of the collar (Pl. XXXI. Fig. 51). In most other species the two structures coincide (see below p. 304). The central canal leading backwards from the neuropore only extends for a short distance, after which the medullary cord is nearly solid, with numerous disconnected vestiges of medullary cavities mostly ill-defined. There may be distinguished two main lateral series of cavities with irregular intervening vestiges. The posterior central canal leading to the posterior neuropore is much longer and more capacious than the anterior canal. There are no roots of any kind.

The dorsal septum extends to the anterior end of the collar nerve-cord appearing immediately behind the anterior neuropore and joining the cord with the basement-membrane of the epidermal involution which is associated with the collar-duplicature (Pl. XXXI. Fig. 51). Posterior to this involution the septum is present but does not reach the epidermis until the level of the buccal orifice of the stomochord is reached, after which its course is uninterrupted to the posterior end of the collar.

The collar canals have the usual semilunar funnel behind which the dorsal wall is invaginated into the lumen of the canal. The dorsal plication is characterised by its tenuity due to the low cells composing it; the remaining walls of the canals consist of high columnar epithelium. The canals open into the first gill-pouch in the normal manner.

<sup>&</sup>lt;sup>1</sup> The perihaemal cavities project forwards for a short distance into the neck of the proboscis. W. III.

In the region of the collar funnels there is a pair of remarkable tubes lying in the perihaemal cavities and opening like the collar canals into the first gill-pouch. These are in fact perihaemal, i.e. **truncal canals** analogous to, and in all probability homodynamous with the collar canals (Pl. XXXII. Fig. 52).

As a rule, as mentioned above, the perihaemal spaces do not contain cavities since they are quite filled up with muscular and connective tissue. In the present species however, while the perihaemal tracts are solid in their anterior two-thirds, posteriorly they develop a cavity which lies between the longitudinal and transverse muscles of the perihaemal coelom (Pl. XXXII. Figs. 52-54). This in itself is an interesting fact, but it becomes still more interesting when, on tracing the cavity backwards, the reason for its existence comes into view in the form of a genuine canalicular extension of the first gill-pouch into the perihaemal coelom on each side. According to Spengel, the collar canals themselves appear to arise as canalicular extensions of the first gill-pouch, and, so far as I can gather, the observations of Bateson and Morgan do not run counter to this view, in essentials.

The truncal canals are smaller both in calibre and in extent than the collar canals and they are not provided with semilunar funnels, and I am not prepared to assert positively that they open into the perihaemal cavities (see, however, Pl. XXXII. Figs. 53—54). But in their quality of canals they are absolutely definite and so far as is known are peculiar to the genus *Spengelia*. No truncal pores have hitherto been described in Enteropneusta, and it is safe to add that none exist in previously known species.

That they existed at one epoch seems likely enough. We have already seen, in the species described in this paper, how that vestiges of different structures crop up in different species.

One species may possess the vestige of a certain structure and another allied species may be without it. It is not probable that truncal canals are essential to one genus and non-existent in any other.

For such reasons as the above I regard the truncal canals of *Spengelia* as being functionally in a vestigial condition and comparable in this and in other respects with the atrio-coelomic funnels described by Lankester in Amphioxus.

The peripharyngeal spaces of *S. alba* commence anteriorly as in *S. porosa*, but they do not end blindly behind as in the latter, neither do they communicate with each other across the ventral middle line; each space passes separately into the trunk coelom, as in *Schizocardium* (Spengel).

The ventral septum only occurs in the posterior region of the collar, commencing a short distance (nearly half a millimetre) in front of the posterior termination of the cornua of the nuchal skeleton.

### TRUNK.

## BRANCHIAL REGION.

The gill-pores of the first pair open coincidently with the posterior neuropore, perforating the posterior commissure of the collar.

The epibranchial band is markedly cristate, the epithelium being thickened in the median line; on the inner surface of the band there is a shallow median longitudinal groove opposite to the crest. The groove flattens out and the crest becomes broader at intervals corresponding with the breadth of a gill-cleft.

The gill-bars are only slightly arcuate. At the medial dorsal angle of every gill-pouch there is a very small diverticulum (Pl. XXXII. Fig. 55). This minute diverticulum of the gill-pouch occupies a position corresponding to that of the large truncal canals described above. It is of course not peculiar to this species, but is particularly well-defined here. It is in such a position that the nephric tubules occur in Amphioxus; and it is possible that at the dorsal angles of the gill-pouches of Enteropneusta we have the makings or the primordia of nephric tubules.

The first gonad on the right side is quite unripe, and I am unable to say whether it is in an incipient or in an arrested state of development; it is connected with the ectoderm between the gill-clefts V and VI.

The second gonad is fully formed and contains ripe spermatozoa; its duct occurs between VII and VIII; the third genital duct is between VIII and IX, and so forth. On the left side there is no unripe anterior gonad like that on the right; the first duct is between VI and VII, the second at the level of VIII, the third between IX and X, and so on.

I have estimated that there are approximately 80 gill-pores on each side. Each half of each gill-cleft is traversed by 10—11 synapticula.

The branchial groove commences in front as a narrow sulcus which gradually widens out posteriorly so that the gill-pores are plainly visible with a simple lens (Pl. XXVII. Fig. 9 A). At its hinder end the groove is as much as '75 mm. in breadth; the gill-pores lie close against the submedian ridge leaving a smooth epidermal tract to form the floor of the branchial groove between the line of pores and the upper margin of the lateral annulations.

## Branchiogenital Transition and Genital Region.

Behind the branchial region the branchial groove is continued into the genital region, not however as a continuous groove but as an interrupted groove traversed by dermal bridges. In this way there is produced the appearance of a series of dermal pits which, as already noted, present externally the same aspect as the dermal pores of S. porosa with which they are evidently homologous, though they are much shallower than the latter (Pl. XXXII. Fig. 59). There are upwards of 25 of these dermal pits on each side (Pl. XXVII. Fig. 9).

In the branchial region there are no medial gonads, i.e. no gonads mediad of the gill-pores, and in the anterior moiety of this region the gonads form a simple lateral series on each side. In the posterior part of the branchial region where the branchial groove widens out, as described above, accessory gonads begin to appear in the space which lies between the main series of lateral gonads and the gill-pores. There may be as many as three accessory gonads in one plane, but they are irregular

in their distribution. Accessory gonads may be observed in various stages of formation, and they certainly appear, in this case, to have an ectodermal origin, being, so far as one can see, primarily in connection with the epidermis.

Bateson also thought it possible that the gonads were ectodermal in origin, while Spengel considered it probable that the germ-cells arise in the first instance in the mesenchyme. Morgan' states that "the gonad is formed from the mesoderm." It seems not impossible that the gonads of the primary series may have a different origin from the accessory gonads when the latter can be shown to be distinct neoformations, as in the present species.

The last gill-slits are quite dorsal in position (Pl. XXXII. Fig. 56) and are followed by a tract comparable to the postbranchial canal of species of *Ptychodera* but not so well-defined.

The dorsal submedian dermal tract below which the accessory gonads occur is characterised both in the posterior branchial and in the genital regions by the attenuation of the subjacent muscular layers. The circular muscles are not interrupted but pass continuously across the tract; the longitudinal muscular bundles are distinctly interrupted, but at the same time straggling fibres are present in greater or less numbers in the tract intervening between the dorsal and the ventro-lateral longitudinal musculature; so that the accessory genital ducts in this species may be said to perforate the longitudinal musculature,

### GENITO-HEPATIC TRANSITION.

This crucial region is characterised in the present species by the occurrence of intestinal canals and pores (Darmpforten of Spengel). Although there are nine pores on each side they occupy a very short tract of the body because they tend to overlap (Pl. XXXII. Fig. 57).

They lie in the submedian tract, i.e. in the line of the gill-pores, although separated from the latter by the whole length of the genital region; their superficial resemblance to the last two or three pairs of gill-clefts is very striking.

Each canal consists of an ectodermal involution which meets and fuses with an outgrowth of the wall of the gut. The lumen of the canal appears more virtual than actual (like that of the genital ducts).

The first pore lies close against the submedian ridge and the succeeding pores occur more and more lateral to this point until a maximum lateral deviation is attained; then the remaining pores successively approach once more the submedian ridge until the last pore is in the same line with the first. The line of pores thus describes an arc which is not in any way due to muscular contraction but is a genuine anatomical feature. The pore-tract occurs at the posterior end of the genital region immediately preceding the hepatic region. It lies a few millimetres in front of the point denoted by an asterisk in Pl. XXVII. Fig. 9, in fact it lies almost in the middle of the sharp curvature which intervenes between the mid-hepatic region (denoted by the asterisk) and the posterior dermal pits shown in the figure. The pore-tract

<sup>&</sup>lt;sup>1</sup> T. H. Morgan, "The development of Balanoglossus," Journ. Morph, 1x, 1894. See p. 60.

may be still further defined as occurring at the level of the anterior dilated end of the ventro-lateral glandless epidermal tract shown in Figures 9 B and 9 c on Pl. XXVII.

Similar pores, in varying numbers, occur in the same region in Bal. meresch-kowskii (Schimkewitsch), Bal. kowalevskii (Spengel), Sch. brasiliense (Spengel) and Gl. hacksi (Spengel). In addition to these paired pores belonging to the posterior end of the genital region Spengel has described a number of similar structures following close behind the branchial region, i.e. at the anterior end of the genital region. These anterior pores may be either paired or unpaired and have been found by Spengel in Sch. brasiliense, Gl. hacksi and Gl. talaboti.

Although generally limited in distribution, in the last-named species they occur in 9 groups distributed at unequal intervals over the anterior four-fifths of the long

genital region.

In Sp. alba the intestinal canals are not provided with a special ring-shaped thickening of basement-membrane such as Spengel has described in Bal. kowalevskii, nor with a sphincter muscle such as occurs in Sch. brasiliense. I have not found any pores other than those here described at the posterior end of the genital region.

Having now become personally acquainted with these remarkable structures, I agree with Schimkewitsch<sup>1</sup>, who was the first to record their existence, in regarding

them as vestigial gill-clefts (see below p. 298).

The hepatic region follows immediately behind the intestinal canals. It is characterised by the presence of internal hepatic saccules having essentially the same topographical relations to the wall of the gut as the hepatic saccules of the Ptychoderidae and Schizocardium, but they are quite internal and are not associated with permanent external sacculation of the body-wall. This is all the more striking because the internal saccules are of large size and perfectly definite; a fact which serves to distinguish this species, and perhaps the genus, from other Enteropneusta.

Although no dermal elevation (or at most a slight arching) accompanies the hepatic saccules we nevertheless find remarkable intersaccular involutions of the epidermis, the walls of which sometimes present complicated corrugations (Pl. XXXII.

Fig. 58).

The occurrence of these intersaccular epidermal involutions would seem to indicate that the external hepatic saccules of the Ptychoderidae are not merely due to the mechanical effect of the hepatic diverticula causing elevations of the skin but have a more fundamental physiological causation. Because it seems probable that the involutions in question are related to the intersaccular, *i.e.* interannular intervals in the Ptychoderidae.

If, as I believe, the Ptychoderidae are relatively primitive, we ought to find vestiges of their hepatic saccules in less primitive forms, and from this point of view we might regard the internal saccules and intersaccular involutions of *Spengelia* as such vestiges.

The ventro-lateral epidermal tract shown in Plate XXVII. Fig. 9 B, 9 c has been referred to above. It is characterised in general by the absence of gland cells and by low cubical or flattened ectoderm similar to that which forms the floor of the dermal

<sup>1</sup> W. Schimkewitsch, "Über Balanoglossus mereschkowskii Wagner," Zool. Anz. xi. 1888, p. 280.

pits. In fact, in section, it appears as a replica of the dorsal submedian tract. Below it the layers of longitudinal muscles is thinner than in the neighbouring tracts and posteriorly this layer thins out almost entirely at this place (Pl. XXXII. Fig. 58). Opposite to the glandless epidermal tract a tract of thickened columnar intestinal epithelium may be observed at the region of the hepato-abdominal transition.

Throughout the entire length of the hepatic region there is a pair of large lateral **splanchnic vessels** lying against the wall of the gut at the outer base of the internal hepatic saccules and at a corresponding level in the anterior abdominal region (Pl. XXXII. Fig. 58). They occupy the position in which a large vessel is often to be seen in *Ptychodera flava* (and doubtless in others) at the base of the lateral septum (cf. Pl. XXIX. Fig. 13). In the Spengelidae there is no lateral septum. A similar pair of vessels has been described by Spengel in *Sch. brasiliense*, *Gl. hacksi* and *Bal. kowalevskii* (Spengel, *Monograph*, p. 575).

## CAUDAL REGION.

The caudal region of S. alba has no very striking characteristics. The longitudinal muscles become feeble and the circular muscles do not suffer any change, there being no special sphincter round the anal opening. There is no band-like or keel-shaped pygochord, but the median ventral epithelial tract of the hind-gut consists of enlarged columnar cells with clear vacuolar contents; it is therefore no doubt to be regarded as a pygochord which has retained its epithelial position in the wall of the gut (Pl. XXXII. Fig. 60).

## OECOLOGY.

The complete unique male specimen which I obtained of this specimen was taken by me from a submerged hillock of sand (resembling a truncated mole-hill) at low water off Vulcan Island (Rakaiya) Blanche Bay, New Britain. It broke itself into three pieces but nothing was lost. The species appeared to resemble Sp. porosa in its mode of life. It is not a burrowing species like Pt. carnosa, but lives in the superficial loose layers of (volcanic) sand like Sp. porosa and Pt. flava.

On account of the length of the proboscis one might suppose, from its external characters, that it was a *Balanoglossus* s. str. It was quite alone although *Pt. carnosa* occurs in the same locality.

### TORNARIA.

A Tornaria which I obtained in the tow-net in Blanche Bay and off the small coral island (Pigeon Island) referred to above, belongs to the group of Tornariae in which the longitudinal ciliated bands are drawn out into tentacular processes.

Spengel calls all such tentaculated Tornariae T. grenacheri, and speaks of their circumtropical distribution (circumterrane Verbreitung) since they have been found in

the tropical regions of all the great oceans, Atlantic, Indian and Pacific.

Spengel does not speak in terms of absolute certainty as to the identity of all the forms designated by the common name T. grenacheri, but gives it as his impression that they are so. In this impression I think he is certainly in error. The name T. grenacheri obviously implies that the forms included under that name are the larvae of one species of Enteropneusta. As a matter of fact there is reason for supposing that Tornaria does not voluntarily migrate far from the habitat of its parent, those which are found at great distances from home having been carried away by currents and doomed to destruction. An instructive example of this is furnished by Agassiz' Tornaria (T. agassizii Spengel) which is sometimes taken off the coast of Massachusetts, and was thought to belong to the Balanoglossus (B. kowalevskii) which occurs on the same coast, until Morgan<sup>2</sup> showed that the latter had a direct development and was in fact identical with the species whose development had been worked out by Bateson.

T. agassizii very possibly belongs to Pt. aurantiaca and is liable to be carried up north by the Gulf Stream.

Pt. biminiensis n. sp. (see below), whose development has been studied by Morgan, possesses a Tornaria of the tentaculated type.

From the small size of the egg it is, I think, quite certain that all Ptychoderidae develop indirectly with a Tornaria larva, and it is probable that the Spengelidae do the same<sup>3</sup>. On the contrary there is no room for legitimate doubt, in consideration of the size of their eggs, that all Balanoglossidae develop directly without a Tornaria.

The Tornaria from New Britain which is here figured most probably belongs either to *Pt. carnosa* or to *Pt. ruficollis*, but it is impossible to say which, because, although I obtained at least one specimen immediately after the metamorphosis, it is notoriously impossible to identify newly metamorphosed larvae of Enteropneusta.

No doubt the differences between the Tornariae of some species are very trifling, but it is a great mistake to imagine that all tentaculated Tornariae belong to one species.

<sup>&</sup>lt;sup>1</sup> This has also been found to be the rule for Echinoderm larvae (Th. Mortensen, *Die Echinodermenlarven der Plankton-Expedition*, 1898).

<sup>&</sup>lt;sup>2</sup> T. H. Morgan, "Balanoglossus and Tornaria of New England," Zool. Anz. xv., 1892, p. 456.

<sup>&</sup>lt;sup>3</sup> The diameter of the ripe eggs of Glandiceps hacksi is about '1 mm. (Spengel).

Among the external points of difference between my Tornaria and the *T. grena-cheri* figured by Spengel may be mentioned those connected with the position of the

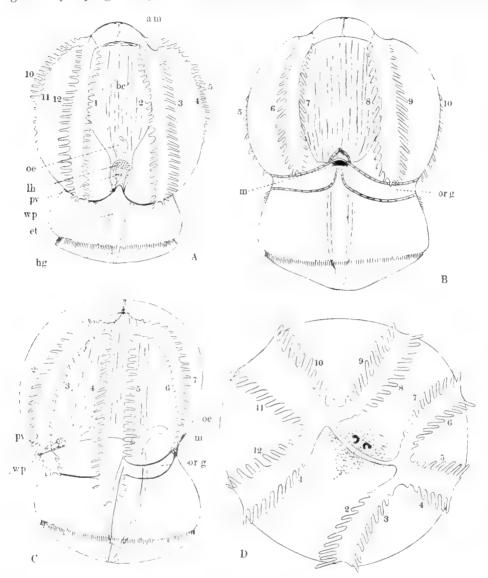


Fig. 4. Tenticulated Tornaria from Blanche Bay, New Britain. Drawn from living larva (January 1895) × about 12. Seen in dorsal view in A, ventral in B, lateral in C, and apical in D. The numbers serve for the identification of the ciliated bands in the different views. The eyes in D are seen to lie within the limits of the ventral area bordered by the ciliated band. In other species they tend to lie centrally between the dorsal and ventral areas.

a.m. Apical muscle-band. bc'. Anterior body-cavity. et. (for st.) Larval stomach. hg. Hind-gut (which contracts and expands as in C). lh. Larval heart (central blood-space). m. Mouth. oe. Larval oesophagus (to which the anterior body-cavity adheres at two points). or.g. Oral groove. pv. Pulsating vesicle (Pericardium, Herzblase). Note its  $\land$ -shape. wp. Water-pore (Sinistral proboscis-pore).

eyes and the inferior dorsal lobe of the ciliated band (Text-figure 4). In my Tornaria there is no such sharply defined lobe, but a groove passes continuously round from the lateral lobe of the ciliated band across the dorsal middle line. This groove is overhung by the anterior body of the Tornaria, and appears in fresh surface view as little more than a line.

In Morgan's Tornaria the dorsal edge of the lateral lobe is entire, there being no inferior dorsal lobe proceeding from it.

The egg of B. kowalevskii (375 mm. in major diameter [Bateson]) is more than six times as large as the egg of Pt. flava and more than four times that of Pt. ruficollis. The egg of Peripatus capensis is not more than five times as large as that of P. novae-britanniae, and the difference in the development of these two species of Peripatus is precisely the difference between direct and indirect development.

Thus both in the Enteropneusta and in the Onychophora the forms whose anatomy leads us to believe are the most primitive are those whose development is indirect, and in both cases it is the indirect development which instructs us as to the proximate affinities of these comparatively isolated groups; while from the direct development we are apparently able to gather information as to the primordial significance of their organisation (e.g. blastopore of P. capensis and coelomic pouches of B. kowalevskii).

<sup>&</sup>lt;sup>1</sup> The fact that we can distinguish between direct and indirect development in an intra-uterine environment is one of very great interest.

## WEST INDIAN ENTEROPNEUSTA.

(Pt. biminiensis n. sp. and Pt. jamaicensis n. sp.)

Only one species of Enteropneusta from the West Indian Islands is described by Spengel, namely, Pt. bahamensis.

Being anxious to ascertain the identity of the species at Bimini which at one time engaged the interests of Professors T. H. Morgan and E. A. Andrews, I wrote to both these gentlemen for information on the subject, and received valuable replies from them which I gratefully acknowledge. Furthermore, Prof. Morgan sent me the collection of adults which still remained to him. The material was, on the whole, in good condition and has been of great use in elucidating the mystery of the proboscis-pore about which I was greatly concerned. Unfortunately the hepatic region was lacking from all the specimens and the diagnostic characters afforded by the genito-hepatic transition are therefore not available. Nevertheless I feel justified in naming two species, although the diagnoses must be imperfect for the present.

The material comprised portions of three species from as many localities, namely, (1) Pt. aurantiaca (Girard) from Beaufort N. C.; (2) Pt. biminiensis¹ n. sp. from Bimini; (3) Pt. jamaicensis n. sp. from Jamaica. They are all Ptychoderidae (this being the information I was at first most anxious to obtain) belonging to the subgenus Tauroglossus; Pt. bahamensis Spengel was not included in the collection.

I am informed by Professor Morgan that the specimens which he generously placed at my disposal were collected by members of the Johns Hopkins Marine Laboratory.

Although the specimens were fragmentary it will be easy to differentiate the two new species from any other known species as well as from each other. If, for convenience, we divide the Enteropneusta into small, large and giant species, then Pt. biminiensis belongs to the category of large forms, while Pt. jamaicensis is a giant species.

Before proceeding to cut this valuable material into sections I experienced great difficulty in finding external differences between the fragments of Pt. biminiensis and those of Pt. aurantiaca, and I accordingly wrote to Prof. Morgan asking whether, in consideration of his personal acquaintance with the living animals, his impression was that the Bimini species was distinct from the Beaufort species. His reply was that he considered the species from the two localities named to be quite distinct, adding the following important point of difference:—"The smell from the Beaufort form is

<sup>&</sup>lt;sup>1</sup> This is presumably the species whose Tornaria development was described by Morgan (Journ. Morph. rx. 1894, p. 1).

overpowering and very persistent even after years in alcohol. The Bahama [i.e. Bimini] worm has quite a bearable stench, very much fainter." In section the difference of the two species is at once evident.

The species of the subgenus Tauroglossus may be arranged into two groups as follows:—

A. Gill-pouches with ventral coeca.

Pt. clavigera, Pt. gigas, Pt. carnosa, Pt. biminiensis and Pt. jamaicensis.

B. Gill-pouches without ventral coeca.

Pt. aperta, Pt. australiensis and Pt. aurantiaca,

or again according to the presence and absence of accessory gonads in the genital region:—

A. With accessory gonads in the posterior branchial and in the genital region.

Pt. aurantiaca, Pt. biminiensis and Pt. jamaicensis, Pt. carnosa (in old animals1).

B. Without accessory gonads.

The remaining species named above, with the exception of Pt. gigas which must be left doubtful in this respect.

# Pt. biminiensis, n. sp.2

The collar has a length of 10 mm. and the proboscis 3.75 mm. in two specimens. The branchial region was much contracted and wrinkled measuring about 40 mm. in length; in the larger fragment about 24 mm. of the genital region remained. In comparison with the following species the most useful measurement which I can state is the width across the expanded genital pleurae, which did not exceed 12 mm. in the alcoholic specimen.

### PROBOSCIS.

Both this and the following species are without the special thickening of the circular muscles at the base of the proboscis which is, according to Spengel, a distinctive feature in *Pt. clavigera*.

## STOMOCHORD.

The region which has been referred to in the preceding pages as the coecal dilatation of the stomochord is, in *Pt. biminiensis*, remarkable for its exceedingly massive development. It recalls somewhat the condition met with in *Pt. carnosa*, especially in regard to the occurrence of dorso-lateral pockets in connection with the dorsal or main division of the lumen of the stomochord (cf. Pl. XXIX. Fig. 17 a and Pl. XXXII. Fig. 65). The dorsal wall of the stomochord in the coecal region is

<sup>&</sup>lt;sup>1</sup> The accessory genital ducts described above in old examples of *Pt. carnosα* do not necessarily and, I think do not in fact, imply the independent origin of additional gonads.

<sup>&</sup>lt;sup>2</sup> For the habits of this species see the following:—T. H. Morgan, "The development of Balanoglossus," Journ. Morph., Vol. 13. 1894, p. 1.

densely packed with mucous cells and at the outer periphery (i.e. the base) of the cells there is a layer of fibrous matter or "Punktsubstanz" like that which underlies the epidermis (Pl. XXXII. Fig. 64). This is a peculiar feature of some importance; it has the same kind of importance as the observation of cilia in this portion of the stomochord of *Pt. carnosa*, namely, a vestigial significance.

In contrast to the massive or sub-solid condition of the stomochord in the coecal region, the anterior portion of the stomochord of this species is distinguished by the spacious cavity which it contains (Pl. XXXII. Fig. 62). The walls surrounding the large cavity are correspondingly thinner than usual, especially the dorsal wall. The central cavity buds off a large number of minute cavities which lie in the thickness of the walls. As we approach the coecal region we find the dorsal wall of the stomochord drawn up into the form of a crest protruding into the central blood-space; the internal basal angles of the crest fuse together so as to constrict off a smaller dorsal portion of the lumen from the wider ventral portion. Farther back the ventral cavity decreases in volume, the walls becoming proportionately thicker until the massive mid-coecal region is reached. When the ventral cavity of the stomochord comes to an end in the anterior part of the coecal region, the stomochord consists of a nearly solid mass of vacuolar reticulate tissue with, however, a small dorsal lumen and minute scattered cavities (Pl. XXXII. Fig. 63).

In its anterior nuchal region the stomochord appears as a flattened transverse band with linear lumen, lying above the body of the skeleton; its dorsal wall is still crowded with mucous cells and the punctate matter is continued.

In the mid-nuchal region, the stomochord is greatly reduced; the mucous cells and fibrous matter disappear and, near the commencement of the wide posterior or buccal portion of the stomochord, the latter is invaded by skeletal substance to such an extent as to cause an interruption of continuity, at least so far as the lumen is concerned. In the posterior nuchal region the walls of the stomochord consist entirely of mucous epithelium, the dorsal wall being much thicker than the ventral. It duly opens into the buccal cavity at the point of bifurcation of the nuchal skeleton.

## NUCHAL SKELETON.

The cupule of the skeleton sends out irregular digitiform processes which penetrate into the substance of the stomochord. One of these processes is shown in Fig. 65, Pl. XXXII. From the dorsal side of the massive body of the skeleton, digitiform processes also project into the anterior nuchal portion of the stomochord; by the cross-fusion of such processes, portions of the stomochord become enclosed within the skeleton. In addition to these stomochordal inclusions, which are confined to the anterior end of the skeleton, there are extensive cellular inclusions within the body of the latter.

There are massive alary processes and a massive keel. The ventral septum of the proboscis ceases close behind the level of the proboscis pore, and the ventral coecum, produced by the confluence of the ventral canals, terminates at the front border of the keel.

### PROBOSCIS-PORE.

Only the left dorsal canal communicates with an end-vesicle; the latter, however, does not end simply at the pore but becomes subdivided by a duplication of the wall into two unequal portions, a smaller right and a larger left moiety. Thus the effect is produced of two pores opening by a common median orifice (Pl. XXXII. Fig. 64). It seems quite obvious that the smaller dextral portion of the end-vesicle corresponds with the dextral vesicle of Pt. flava. The slit-like pore of the left portion is longer than that of the right, but both portions of the end-vesicle have long post-trematic coecal extensions (the left rather longer than the right) which lie on either side of the forward extremities of the perihaemal cavities. The smaller dextral portion maintains a more dorsal position than the bulk of the larger sinistral portion. The latter extends backwards beyond the region of the anterior neuropore.

Thus there is, in effect, a dextral end-vesicle and a dextral pore without any vestige of connection with the right dorsal proboscis canal. The pronounced subdivision of the end-vesicle in this species throws light upon the less complete subdivision observed in *Pt. carnosa*. The peculiar conditions here described are still more clearly established in the species next dealt with.

### COLLAR.

### NERVE-CORD.

There is no median anterior neuropore in this species; the medullary cord closes in solid in the anterior median tract but there are two short lateral cavities bounded by numerous mucous cells (Pl. XXXII. Fig. 65). These paired cavities open in front and are essentially due to the backward continuation of the dorso-lateral angles made by the union of the neck of the proboscis with the collar flap. This is a clear and instructive example of the way in which a median structure can assume a paired form.

The main body of the collar nerve-cord is practically solid, the medullary cavities being reduced to the merest vestiges. It is also characterised, in its anterior third, by the presence of a large quantity of yellowish flocculent tissue, the bulk of which forms a tract on each side of the middle line. In front, the cord is sub-triangular in section, the ventral angles being produced downwards so as to form bold projections into the perihaemal cavities; behind the orifice of the stomochord, these ventral horns of the medulla flatten out and the cord then becomes a transversely elliptical band.

The first and only **root** is massive and sub-solid; it has a backward course along the anterior free edge of the dorsal septum and occurs in front of the orifice of the stomochord.

The dorsal septum only extends for a short distance behind the root, when it becomes interrupted and finally disappears only to reappear near the posterior end of the collar in the region of the well-defined wide posterior central cavity of the nervecord which duly opens by the posterior neuropore.

## TRUNK.

All that need be said, and indeed in view of the fragmentary character of the material, the most that can be said as to the peculiarities of the truncal region of *Pt. biminiensis*, relates to points which have been already mentioned, namely, the occurrence of ventral diverticula of the gill-pouches and the presence of accessory gonads in the posterior branchial and genital regions.

It is only necessary to add, with regard to the accessory gonads, that they do not occur mediad of the main series, but only laterally, and they lie entirely within the genital pleurae<sup>1</sup>. This is an important difference between this species and Pt. aurantiaca where, as Spengel has shown, the accessory gonads occur both laterally and medially, i.e., on both sides of the main series. In front the gonads commence some distance behind the posterior rim of the collar.

I think it has been made sufficiently clear that this is quite a distinct species. Should the opportunity present itself to any naturalist visiting the Bahamas, particularly the Bimini Lagoon, to make further observations, it is desirable to note the external character of the genito-hepatic transition, the proportionate lengths of branchial and genital regions and, in section, the nature of the pygochord, if one occurs.

## Pt. jamaicensis, n. sp.

In the single specimen at my disposal, the proboscis was nearly concealed within the collar-flap. The collar was much wrinkled and contracted to a length of about 1 cm.; the width was greater than the length in the contracted state.

The width of the body in the branchial region, with closed genital pleurae, was 11 mm., and the vertical height, under the same conditions, was 17 mm. The width across the expanded genital pleurae was 29 mm. This species therefore belongs to the category of giant forms.

Professor E. A. Andrews has kindly supplied me with notes as to the appearance of this species during life together with some sketches, from which I gather the following details. "Balanoglossus very abundant in sandy cove on north [side] of Drunken Man Cay, off Harbour of Kingston." It lives in coral sand. "Only tail end usually cut off by spade; two ? heads taken in 3—4 hours." "Colour, yellowish white, with conspicuous transverse bands of red-brown arranged alternately" on the two sides of the body.

On one side of the body (? dorsal) these pigmented bands end sharply at the sides of the median groove; on the opposite side they bend forwards (or backwards) and their ends break up into a number of spots on either side of the median line. On the side on which the pigment-rows break up into spots, the body is "covered by numerous rounded, blunt papillae [dermal islets]; each [papilla] shows, under lens, minute white specks," probably due to mucous glands.

<sup>&</sup>lt;sup>1</sup> Of course this statement does not refer to the normal medial branch of the lateral gonads which always occurs on the mesial side of the lateral septum.

"Proboscis small, collar large; with no colour, except uniform yellow and fleshy." The pigmented bands were visible in some of the pieces of the abdominal region in the preserved condition.

Apart from the differences in size and colour-markings there are but few characters which can be definitely stated to establish a specific distinction between the present species and Pt. biminiensis. The impression produced upon the naturalists who collected both species was that they were distinct, and I have thought it would serve the interests of the subject best, under the circumstances, to give them separate names. It is only necessary to remember that Pt. jamaicensis may stand in a similar relation to Pt. biminiensis to that which Pt. robinii (Giard) bears to Pt. clavigera (Delle Chiaje), or Bal. mereschkowskii Nic. Wagner to Bal. kowalevskii Agassiz.

It is true that there is a striking difference in the matter of the proboscis-pores, but such as it is, it is only due to an exaggeration of the condition observed in *Pt. biminiensis*. In the present species there are two distinct end-vesicles and two proboscis-pores. At the level of the pores, the vesicles are nearly equal, but the prae-trematic portions of the vesicles are unequal, the bulk of the left exceeding that of the right. Only the left vesicle is in communication with the proboscis coelom; the right vesicle is blind at both ends. I say at both ends advisedly because in the case of both right and left vesicles, there is a long coecal post-trematic extension, stretching a considerable distance beyond the level of the anterior neuropore, and hence underlying the medullary cord.

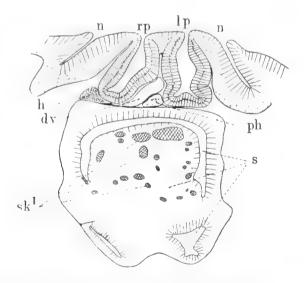


Fig. 5. Transverse section through the proboscis-pores and neuropore of Pt. jamaicensis.

dv Dorsal vessel (at the point where it passes into the central blood-space and gives off the advehent dermal vessel of proboscis). h Pericardium (solid posterior extremity). lp Left proboscis-pore. rp Right proboscis-pore. n The two halves of the neuropore. ph Perihaemal space (anterior extremity). s Stomochord.  $sh^1$  Skeletal inclusions in the stomochord (due to digitiform processes from the cupule of the nuchal skeleton).

As shown in the text-figure, the proboscis-pores occur approximately at the level of the neuropore, although the latter is subdivided in this species in the same way as in *Pt. biminiensis*.

The digitation of the cupule of the nuchal skeleton is also more extensive in the present than in the preceding species. The stomochord undergoes fragmentation in its nuchal region by the invasion of strands of skeletal substance, very much as in *Pt. carnosa*.

The collar nerve-cord in its middle portion consists of a sub-solid transversely flattened band. There is a single root arising from the cord immediately in front of the buccal orifice of the stomochord; it passes directly to the epidermis with which it unites by a long anteriorly directed apical border. There is no dorsal septum near the root; it is limited to the posterior quarter of the nerve-cord.

As already mentioned, the gill-pouches are produced ventrally into coecal prolongations. The gill-clefts are traversed by upwards of 50 pairs of synapticula.

In the portion of the body which is characterised by the presence of the lateral septa, namely, in the posterior branchial and genital regions, accessory genital ducts occur laterally from the main series. The accessory gonads are arranged in a radial manner in the genital pleurae and entirely fill the latter. The genital region of the preserved animal was very brittle and the layers of the body-wall were in a disrupted condition, but I have been able to satisfy myself, with reasonable certainty, that this species agrees with  $Pt.\ biminiensis$  in having only lateral accessory gonads.

The specimen at my disposal was a mature female. The ova were tightly packed together, causing them to assume polygonal shapes, and they measured '11 mm. in diameter.

As at least two kinds of Tornaria have been recorded from the West Indies it is important to note that, so far as known, all the Enteropneusta inhabiting the shores of these islands belong to the family of the Ptychoderidae.

# MORPHOLOGY OF THE ENTEROPNEUSTA.

In his monumental monograph of the Enteropneusta, Professor Spengel was led to negative conclusions as to the outside affinities of the group. This result may be partly accounted for by the fact that he was handicapped in being obliged to make use of an unsuitable form, namely, Ptychodera minuta (the common species of the Bay of Naples), as the basis of his work. I cannot help thinking that the theoretical aspect of his labours might have assumed a different complexion if he could have started with such a form as Ptychodera flava.

As a treasury of facts it would not be easy to overestimate the value of this, the eighteenth monograph issued by the management of the Zoological Station at Naples; and I hope I have made it clear in the foregoing pages, how much later workers, like myself, are indebted to Professor Spengel for the great work which he has accomplished.

The result of my own observations, which have, intermittently, extended over the best part of three years<sup>1</sup>, has been not only to confirm my belief in the theory of the Chordate affinities of the Enteropneusta, which was first definitely advocated by Bateson, and has been accepted by most, if not all subsequent naturalists who have dealt with the group, with the exception of Spengel, but, to carry to my own mind the conviction that the Enteropneusta stand much nearer the direct line of Chordate descent than has generally been supposed.

Perhaps it may be admitted that I have brought forward a sufficient number of new facts to justify a restatement of the case for the Enteropneusta.

The views contained in Bateson's standard work on the direct development of Balanoglossus (published during the years 1883—1886) were naturally and properly based upon similarity of structure and origin. Spengel denied this similarity since it fell short of identity. It now remains to found the theory upon change of function. Such a theory not only dispenses with the necessity of the identity of structures, in widely separated forms, which are supposed to be genetically related, but it requires that they should be different.

I think it right to assume that it would be quite out of place for me to attempt the formidable task of discussing Dr Gaskell's Theory of the Origin of Vertebrates<sup>2</sup>. I have quite enough on my hands in stating the case for the Enteropneusta. I may be permitted to say that I, for one, regard Dr Gaskell's work as an important contribution to the history and theory of the subject. Dr Gaskell has himself spoken of his theory as an "earthquake hypothesis," and it may probably be regarded as the culmination of that line of thought (namely, the reference of the Vertebrata to an Articulate ancestry) which originated with Ét. Geoffroy St. Hilaire and has numbered

<sup>1</sup> I made the acquaintance of Pt. flava in July 1896.

<sup>&</sup>lt;sup>2</sup> W. H. Gaskell, "On the origin of Vertebrates, deduced from the study of Ammocoetes," Journ. Anat. and Physiol., Vol. xxxII., p. 513 and Vol. xxxIII., p. 154.

among its adherents Leydig, Semper, Dohrn, Eisig and many other distinguished names.

Without presuming to characterise the present contribution as a culmination of any kind whatever it may nevertheless be said, with truth, that it falls into line with the work of Johannes Müller, Kowalevsky, Hatschek, Huxley, Lankester and others.

## I. THEORY OF GILL-SLITS1.

In submitting the theory of gill-slits at which I have arrived during the course of my work on the Enteropneusta I definitely assume, at the outset, that whatever be the true approximate explanation of gill-clefts, it must, at all events, be sought for in free-living animals possessing a straight alimentary canal and not in sedentary forms, nor in purely pelagic forms, which possess a U-shaped alimentary canal. The theory suggested by Harmer based upon the anatomy of Cephalodiscus and by Brooks on the basis of Appendicularia, which has recently been further elaborated by Masterman<sup>2</sup>, does not, in my opinion, account satisfactorily for the primordial origin of gill-slits, but it probably does explain the retention of a single pair of gill-clefts in the above-named animals. This is a point of great interest and some importance, because, the Pterobranchia probably bear the same sort of relationship to the Enteropneusta as that in which the Urochorda stand to the Cephalochorda.

In the Enteropneusta, as in Amphioxus, we observe the very remarkable phenomenon of the coincidence of the branchial and genital regions.

Whereas in the craniate Vertebrates the gonads have absolutely nothing to do with the branchial region, in these primitive groups of the Enteropneusta and the Cephalochorda, gonads and gill-slits are, roughly speaking, coextensive.

The intrinsic importance of gill-slits is abundantly evident from one of their most fundamental properties, namely, their persistency. Whereas teeth, limbs, limb-girdles, digits, etc., after having been once acquired, have been secondarily lost, over and over again, without leaving so much as a trace in the individual ontogeny, gill-slits persist throughout the whole series of craniate Vertebrates, into the human foetus.

The Memoria technica given below serves to illustrate the position of the Enteropneusta in the natural system; and also the dual propensities of this group towards the Echinoderms on one side and the Chordata on the other. The only liberties I have taken are firstly to introduce two new collective names, one of which, Branchiotrema, is to include all animals which possess gill-slits at any time in their life-history; and secondly to apply the name Bilateralia of Metschnikoff somewhat differently from what was originally intended. It is a poor word in any case to apply to a limited group of animals<sup>3</sup>, but its retention recalls the fact that Metschnikoff first discovered the

<sup>&</sup>lt;sup>1</sup> The substance of the remarks which follow under this heading was given in a paper read before the Cambridge Philosophical Society on Nov. 14th, 1898 (see *Proc. Camb. Phil. Soc.* Vol. IX., 1899, p. 37.)

<sup>&</sup>lt;sup>2</sup> A. T. Masterman, "On the further anatomy and the budding processes of Cephalodiscus dodecalophus M'Intosh." Trans. Roy. Soc. Edinb., Vol. 39, 1898, p. 507.

<sup>&</sup>lt;sup>3</sup> Metschnikoff called the Enteropneusta, Bilateralia, and included them with the group of the Echinoderma under the phylum or sub-phylum Ambulacralia.

metamorphosis of Tornaria and that he, like his successors Bateson, Morgan (loc. cit.), MacBride¹ and others, believed in the special though remote genetic relationship of the Enteropneusta and Echinoderma; the name is also useful as a reminder of the supposed bilateral ancestry of the Echinoderms.

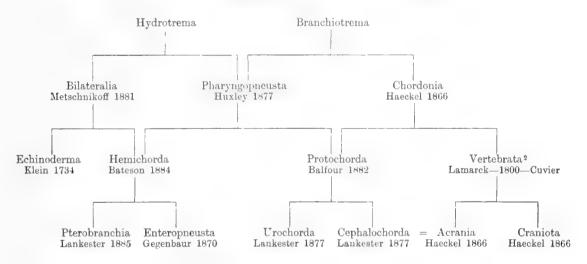
The other collective name which I have suggested, viz. **Hydrotrema**, will be justified in the sequel.

With regard to the introduction of the name, Branchiotrema, I will say that there is just as much or as little need for this addition to our terminology as there was for Huxley's Pharyngopneusta. Moreover, assuming that the knowledge of these creatures which has accumulated during the last thirty years or so, is not illusory, I think that the conception contained in this term, namely, that gill-slits have the priority of the notochord, will turn out to be well-grounded.

A table, such as the one given here, brings out the dual or overlapping propensities of the various groups in a way which is not possible in an ordinary classification.

### MEMORIA TECHNICA

### RELATING TO THE CHORDATE SERIES OF ANIMALS.



The theory for which I shall proceed to point out the evidence may be briefly stated as follows:—The gonads and gill-slits were primarily unlimited in number and coextensive in distribution, the gonads having a zonary disposition and the gill-slits occupying the interzonal depressions. The primary function of the gill-slits was the oxygenation of the gonads, their secondary function being the respiration of the individual.

Perhaps it will be best to deal with the evidence categorically.

<sup>&</sup>lt;sup>1</sup> E. W. MacBride, "The development of Asterina gibbosa." Q. J. M. S., Vol. 38, 1896.

<sup>&</sup>lt;sup>2</sup> Holochorda of Gadow and Masterman. (H. Gadow, A Classification of Vertebrata, London, 1898. A. T. Masterman, "On the Diplochorda," Quart. Journ. Micro. Sci., Vol. xl., 1897.)

## A. EVIDENCE OF UNLIMITED GILL-SLITS.

The evidence is of various kinds and derived from various sources, e.g. number, formation, limitation and vestiges of gill-clefts.

a. Number and formation of gill-slits. It is a fact which sharply distinguishes the Enteropneusta and Cephalochorda from the craniate Vertebrates that new gill-slits are added at the posterior end of the pharynx throughout life.

In spite of this successive addition, at longer or shorter intervals, there is in most cases a maximum which is usually not overstepped before death ensues. In Amphioxus the maximum may be taken as from 90 to 100 gill-slits on each side. In Pt. flava the number of gill-clefts acquired by the macrobranchiate forms may be taken at about 150 pairs. In Pt. aurantiaca, according to Spengel, the gill-slits may reach the impressive total of 700 pairs. In this case it appears to be impossible to assign a maximum. Pt. minuta goes to the other extreme and never has more than 40 pairs (Spengel).

β. Limitation of gill-clefts. The fact of limitation is shown in absolutely unequivocal manner within the group of the Enteropneusta. It is implied in the facts given in the preceding paragraph which might easily be supplemented. It is however sufficient to compare the conditions met with in Pt. flava and Pt. ruficollis respectively. Whereas the length of the pharynx of Pt. flava varies enormously, namely, from less than a centimetre up to about 3 centimetres, that of Pt. ruficollis is remarkable both for its shortness and its constancy (cf. Pl. XXVI. Figs. 1 and 2; and Pl. XXVII. Fig. 7).

If further demonstration of limitation be required it is furnished in a totally unexpected way by the **postbranchial canal** of *Pt. ruficollis* as compared with the corresponding portion of the gut in *Pt. flava* and *Pt. carnosa*. In the two lastnamed species the last pair of gill-slits occurs at the dorso-lateral margins of this structure and new slits are duly added in line with the pre-existing slits. In *Pt. ruficollis* the gill-slits have nothing whatever to do with the vestigial postbranchial canal, the last few pairs opening at the base of it directly into the ventral division of the gut. This faculty of the gill-slits of shifting their position and having their primary topographical relations radically changed is worthy of particular note. At the posterior end of the pharynx in *Pt. ruficollis* the gill-slits have, in effect, moved from a dorsal to a more ventral position (Pl. XXX. Figs. 32, 33).

γ. Vestiges of gill-clefts (see also below p. 321). Under this head are probably to be placed the **intestinal pores** (Darmpforten) originally discovered in Balanoglossus mereschkowskii by Schimkewitsch, whose observations were greatly extended by Spengel. They occur in certain species only, namely, Schizocardium brasiliense, Glandiceps talaboti, Gl. hacksi, Bal. kowalevskii and Bal. mereschkowskii, and in my Spengelia alba (see

<sup>1</sup> Spengel says Bal. mereschkowskii (the White Sea Enteropneust) is probably co-specific with Bal. kowa-levskii.

above and Pl. XXXII. Fig. 57). Both Schimkewitsch and Spengel admit the possibility of these pores being related in one way or another to gill-slits.

There may be two sets of pores, anterior and posterior. The anterior pores, when present, follow close behind the branchial region and the posterior pores occur at the genito-hepatic transitional region.

Intestinal pores do not occur in the Ptychoderidae.

What we do find, however, in the Ptychoderidae are the remarkable ciliated grooves of the intestine, with their medially placed covering-pads extending (e.g. in Pt. flava) from the anterior end of the hepatic region to the posterior end of the abdominal region, but not into the caudal region. In the subgenus Chlamydothorax (as shown by Spengel in Pt. erythraea and as I have found in Pt. flava), the ciliated grooves are not simple longitudinal furrows but undergo metameric or interannular sacculations. These sacculations often approach very closely to the epidermis. They strongly resemble a gill-pouch before its perforation to the exterior such as I have described in Pt. flava. The medial covering-pad often suggests a tongue-bar. (Cf. Pl. XXIX. Figs. 12—14.)

It is not unlikely that these sacculations of the ciliated apparatus of the gut in the subgenus *Chlamydothorax* are homodynamous with the gill-pouch diverticula of the gut and, in this quality, are the vestiges of gill-slits which doubtless formerly extended throughout the greater part or the whole of the trunk. *Pari passu* with the phenomenon of cephalisation, a process which has always been at work in the evolution of Metazoa, the primarily unlimited gill-clefts became limited to the anterior region of the trunk.

## B. COEXTENSION OF GILL-SLITS AND GONADS.

The above conception of the limitation of the gill-clefts to the anterior region of the trunk in correlation with cephalisation and regional differentiation is in accordance with what happens in the Craniota. What is not in accordance with craniate traditions is the fact that as a first stage in the process of limitation or localisation of the gonads, they were likewise restricted equally with the gill-slits to the anterior end of the trunk. Whereas in Amphioxus the number of gonads is strictly limited and constant, being laid down once for all during the early adolescent phase of development, in the Enteropneusta the formation of gonads goes on throughout life. As stated by Spengel, the principal point of origin of new gonads of the primary or lateral series is at the posterior end of the gonadial series. As is known new gill-slits arise exclusively at the posterior end of the branchial series.

It is hardly necessary to dwell at length upon the coextension of gonads and gill-slits since it is such an obvious fact, and is practically implied in Spengel's term branchiogenital region. It is none the less remarkable because it is obvious. The reason why we seldom find exact coextension of gill-slits and gonads is because another factor has been at work which has resulted in the more or less complete emancipation of the gonads from the gill-slits (see below). However, there is one admirable example of complete coincidence of branchial and genital regions, namely Balanoqlossus canadensis Spengel.

## C. Annular ridges and Interannular depressions.

The skin of the Enteropneusta is particularly characterised by the thickened glandular epidermal patches which are arranged in a more or less regularly zonary manner so as to produce the appearance of raised glandular annulations separated from one another by interannular non-glandular grooves. These annulations extend from end to end of the trunk.

In the hepatic region of the Ptychoderidae the apparently unimportant, but nevertheless ever-present, epidermal annular ridges are drawn into the service of the hepatic diverticula of the gut, whose outer free edges they bound. The external liver-saccules of the Ptychoderidae are, outwardly, nothing else than products of local hypertrophy of the annular ridges, while the intervals between the successive saccules are the usual non-glandular interannular tracts.

The **epidermal zonulation** of the Enteropneusta is usually quite unjustly treated as having no deep-lying significance at all.

We have seen what can become of the annular ridges, but it is of more importance for my present purpose to point out some of the potentialities of the interannular grooves or tracts.

The dermal pits of Spengelia are local intergonadial depressions of the interannular tracts.

In Sp. porosa the last gill-slits open at the base of the most anterior pits. The succeeding pits, although they approach near to the wall of the gut, do not meet it. If they did meet it they would probably fuse with it and form gill-slits.

It would conceivably need but a comparatively slight functional stimulus to induce either a pre-existing gut-sacculation to fuse with the epidermis or a pre-existing dermal pit to fuse with the gut-wall. But when dermal depressions and gut-sacculations coincide, then perforation is almost certain to follow sooner or later. It may readily

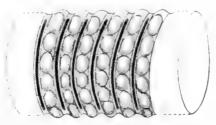


Fig. 6. Diagram to illustrate the theory of the primary intergonadial position of the gill-clefts. No insistence is placed upon the subdivision of the gonads into superposed follicles. They are thus represented in order to illustrate more clearly the principle of zonulation.

be observed that the wall of the gut is thrown into transverse folds producing crests and valleys. This is especially well seen in a large form like *Pt. carnosa*. The gut of the Enteropneusta is intrinsically straight; at the same time it is necessary to have as large a digestive surface as possible on account of the nature of its food. It effects increase of surface by means of such transverse or circular or zonary plications<sup>1</sup>.

<sup>&</sup>lt;sup>1</sup> Spengel points out that in Bal. kowalevskii and Bal. kupfferi the intestine is considerably longer than the body, and hence has a serpentine course (Schlängelung des Darmcanals).

### D. OXYGENATION OF THE GONADS.

By pressing the gill-slits at their first origin into direct functional relation with the gonads we only assign to them their pre-eminent importance in the economy of the higher animals and to that extent we explain their persistency. There is no need to insist upon the truism that the possibility of progressive evolution is dependent upon the gonads being exposed to the best possible physiological conditions.

In my previous paper on Spengelia (loc. cit.) I stated that the dermal pits apparently served for the irrigation of the gonads. At that time I had no idea of framing an elaborate theory of gill-slits.

What induced me to venture upon such treacherous ground was the zonulation of the gonads in the genital pleurae of *Pt. flava* and the reflection brought home by the exposed pharynx of this species that the septal bars corresponded, in principle, with the annular ridges of the body-wall while the gill-clefts took the place of the interannular depressions<sup>1</sup> (Pl. XXVI. Figs. 1, 2).

## E. EMANCIPATION OF THE GONADS. LATERAL SEPTA.

The primary relation of gill-slits and gonads which the present theory assumes is not exactly retained in any existing form that we know, although it is suggested by many tangible facts. The gonads have become emancipated from their direct dependence upon the gill-slits for their oxygenation concomitantly with the elaboration of the vascular system. This emancipation has taken place in two ways, firstly by their relegation to **pleural folds** of the body-wall and secondly by their **recession** from the branchial region.

The regional differentiation of the body is one of the cardinal features in the organisation of the Enteropneusta, but it is not complete since the regions tend to overlap. But whereas it is usually possible to define a genital region between branchial and hepatic regions, in the subgenus Chlamydothorax this is not possible; because, although there is a short tract intervening between the pharynx and the hepatic region, the gonads have no more to do with this tract than they have with any other portion of the body proper. In this subgenus the gonads have become abstracted from the main trunk and are confined to special pleural folds. That the genital pleurae are structures superadded to the main body of the animal is evident from the behaviour of the lateral septa which are an exclusive appanage of the Ptychoderidae.

Where the genital pleurae are at their maximum, namely in Chlamydothorax, the lateral septa likewise have their greatest development. In Pt. flava the lateral septa are coextensive with the genital pleurae because the latter are quite independent of the branchial region. In other forms the lateral septa cease in the posterior portion of the branchial region. The lateral septa are vascular folds of the basement membrane

<sup>&</sup>lt;sup>1</sup> This impression is made all the stronger by the fact, already mentioned, that the tongue-bars are not visible in the external view of the pharynx of preserved specimens owing to their deeper position. Only the septal bars and the intervening slits are visible in such a view.

which accompany the genital pleurae and carry the genital blood-vessels. They mark out the path of emancipation of the gonads from the gill-slits<sup>1</sup>.

In other existing forms, excepting Bal. canadensis<sup>2</sup>, the genital pleurae have undergone progressive reduction (from before backwards) with the result that the gonads have become to a greater or less extent secondarily restored to the main body of the animal and the gill-slits have been closed in laterally, their external openings being reduced to minute pores placed dorsally on each side of the dorsal nerve-cord.

The gonaducal (submedian, Spengel) line is that in which the genital pores are placed and it coincides with the series of gill-pores except in those Ptychoderidae which possess genital pleurae. The gonaducal line of the Ptychoderidae is further denoted by the peripheral insertion of the lateral septum into the basement-membrane of the epidermis. This line in Chlamydothorax occurs at or near the dorsal free edge of the genital pleurae. In Tauroglossus, where the gonads lie partly in the pleural folds and partly in the main body-cavity, the gonaducal line has shifted from the summit nearly to the base of the genital pleurae<sup>3</sup>. Finally in such a species as Pt. ruficollis, where there are no genital pleurae in the branchial region, the gonaducal line and branchial groove coincide.

Having been secondarily restored to the main body-cavity the gonads have apparently been exposed to the influence of another set of changes tending to their further limitation to a definite genital region.

I refer to the **recession of the gonads** from the branchial region. In comparatively few forms do the gonads extend to the extreme anterior end of the branchiogenital region. They do so in *Pt. minuta* and *Pt. flava* and a few others; but as a rule they commence at various distances from the posterior rim of the collar. This is best shown in tabular form.

## TABLE SHOWING RECESSION OF THE GONADS.

| Pt. ruficollisFirst genital duct between 5th and 6th gill-pores.                                    |
|---|
| Pt. sarniensisFirst genital duct beside the 20th gill-pore, about 4 mm. behind collar. [Spengel.]   |
| Pt. aurantiacaGonads commence some millimetres behind collar; in branchial region they are          |
| arranged in a single series and in the genital region in multiple series.                           |
| [Spengel.]  |
| Sch. brasilienseGonads commence about level of 15th gill-pore. [Spengel.]                           |
| Sch. peruvianumGonads not present in fragment in which 70 pairs of gill-clefts occurred. [Spengel.] |
| Gl. hacksi  |
| region. In young specimen they commenced at the level of 13th—14th                                  |
| gill-pores. Thus the most anterior gonads of adult are added secondarily.                           |
| [Spengel.]  |
| Gl. abyssicola  |
| recession complete. [Spengel.]  |
|   |

<sup>1</sup> Just as recurrent nerves show divergence from primitive topographical relations.

Pt. flava......Coextensive with genital pleurae.

<sup>3</sup> This shifting of the gonaducal line (cf. Pl. XXVIII, Fig. 6 and Pl. XXX, Fig. 23) may also be regarded as evidence of the possibility of change of function of the genital pleurae (cf. p. 317).

<sup>&</sup>lt;sup>2</sup> Bal. canadensis, as described by Spengel, is a most interesting and peculiar species. It possesses two sets of pleural folds which contain the gonads, dorsal and ventral. The genital blood-vessels of this form constitute a system sui generis, and there are no lateral septa.

#### SUMMARY.

- 1. My view is that the gill-slits arose originally as perforations in the interannular grooves for the aeration of the gonads which occupied the dividing ranges.
- 2. In the existing Enteropneusta the gill-slits no longer serve this primary function directly, since there is an elaborate and highly peculiar vascular system.
- 3. Consequently in the most primitive forms (e.g. Pt. flava) we find the gonads quite removed from the neighbourhood of the gill-clefts and relegated to pleural folds of the body.
- 4. When secondarily restored to the main body-cavity owing to reduction and disappearance of the pleural folds, there is a tendency for the gonads to restrict themselves to a special region of the body, or in other words, to withdraw themselves from the branchial region.
- 5. This withdrawal of the bulk of the gonads from the branchial region manifests itself in different ways:—
- (i) By reduction of the ramifications of the gonadic pouches in the branchial region<sup>1</sup>.
  - (ii) By removal from anterior end of trunk.
  - 6. The theory may be represented in tabular form as follows:-

### GILL-SLITS.

Primary function = Oxygenation of gonads.

Secondary function = Respiration of individual (Primary function superseded by elaboration of vascular system).

Primary position = Intergonadial.

Secondary position = Segmental.

Primary number = Unlimited and indefinite.

Secondary number = Limited and definite.

## GONADS.

Primarily coextensive with gill-slits.

- A. Unlimited.
- B. Limited.

Secondarily emancipated from gill-slits.

- A. Restricted to genital pleurae.
- B. Restricted to genital region.

<sup>&</sup>lt;sup>1</sup> Besides Bal. canadensis already referred to, Bal. kupferi is exceptional in that the gonads attain their maximum development in the branchial region (Spengel).

## II. PROBOSCIS-PORES AND ANTERIOR NEUROPORE.

Spengel rejects the idea of anterior and posterior neuropores and describes instead anterior and posterior epidermal invaginations or pouches (vordere und hintere Epidermistasche) at the two ends of the collar nerve-cord. We will consider first of all the anterior pore alone. "Bei allen Arten der Gattungen Balanoglossus und Glandiceps," says Spengel (Mon. p. 606), "also derjenigen, bei denen bis jetzt kein typischer Axencanal beobachtet worden ist, besteht dorsal von der Ansatzstelle des Eichelhalses an den Kragen eine bald tiefere, bald flachere trichterförmige Einsenkung der Haut, eine blind endigende, von Epidermis ausgekleidete Tasche, welche bis ans vordere Ende des Kragenmarks reicht."....." Was aber mehr als alles andre den Ausschlag zu Gunsten der soeben vorgetragnen Auffassung giebt, das ist der Umstand, dass manchmal im Bereiche dieser Tasche die Eichelporen gelegen sind" [e.g. Bal. canadensis, Gl. talaboti]......" Ein etwas abweichendes Verhalten zeigt die Epidermistasche bei Schizocardium brasiliense. Hier trifft nämlich ihr Ende nicht auf das Vorderende des Kragenmarks, sondern sie erstreckt sich dorsal vom Kragenmark ein Stückchen über diesen Punkt hinaus, so dass das Kragenmark [which here is solid] sich der ventralen Wand der Tasche anheftet. Man könnte auch sagen, die Tasche sei mit einem dorsal vom Kragenmark in die Cölomhöhle hineinragenden Blindsäckchen versehen. ist es bei Sch. peruvianum."

My observations on Spengelia alba allow me the satisfaction of admitting that what Spengel says is true. Only it is not the whole truth. The conditions in Sp. alba which I have described above on p. 279 show that the anterior neuropore, as it occurs in most Enteropneusta, is not a simple structure but that it has two-fold significance which is frequently masked. When it reveals its double nature indirectly or in half-measures, it is perplexing and tends to lead to confusion. It may be said to have done this in the case of the species named in the passages from Spengel which I have quoted above.

In Sp. alba we find the double nature of the anterior neuropore exhibited unequivocally, in that a true neuropore (s. str.) coexists, independently, with an anterior epidermal invagination (cf. Pl. XXXI. Fig. 51).

In most cases the neuropore and the epidermal ingrowth coincide (e.g. Pt. flava); in some cases the neuropore is obsolete and only the epidermal pouch remains (e.g. Schizocardium); in rare cases the neuropore and epidermal pouch are both present and distinct from one another (e.g. Sp. alba); in no case, among the Enteropneusta, can the epidermal pouch be said to be entirely absent simply because there is always a niche formed at the point of insertion of the neck of the proboscis into the dorsal wall of the collar.

Thus we see that there is no fault to be found with the "anterior neuropore" on the one side, nor with the "vordere Epidermistasche" on the other. It is only necessary to bear in mind that there is a neuropore (s. str.) and also an epidermal

pouch to be taken into consideration. When this has once been recognised it is allowable to use the expression "anterior neuropore," in the wider sense, to cover the two structures which, in the Enteropneusta, usually combine to produce it, but which sometimes assert their independence.

Spengel (Mon. p. 470) points out that where two proboscis-pores occur in the adult it is highly probable that the dextral pore has a secondary origin in an

ontogenetic sense, as no Tornaria has ever been found with two water-pores.

This is probably true for those forms which pass through an indirect development. Thus we are, for example, bound to assume that the Tornaria of Pt. flava possesses a single sinistral pore. With those Balanoglossidae which possess two pores, namely, Bal. kupfferi and Bal. canadensis, the matter is different and I should be prepared and even expect to find that in those species, having a direct development, the two pores would arise together as they do in regenerating specimens of Pt. flava. It is sufficiently clear that the paired condition of the pores is phyletically the more primitive, and Spengel intimates that he is likewise of this opinion. We have therefore here a very interesting example of a phyletically older condition being recapitulated as a secondary ontogenetic phenomenon<sup>2</sup> (cf. above Pt. carnosa).

The comparative morphology of the proboscis-pores is a subject of almost discouraging complexity; and the attempt to elucidate it makes no light task.

Three facts, inter alia, which have come under my observation, have conducted me to certain ideas which, so far as they go, are quite clear and definite in my own mind. These facts are:—

- 1. The terminal tubular vesicle or end-sac which typically opens internally into the proboscis coelom and externally by the proboscis pore, may be quite shut off from any communication with the coelom; in other words, it may be completely emancipated from the coelom (Pt. flava, Pt. jamaicensis).
- 2. The end-sac<sup>3</sup> may have a comparatively long post-trematic coecal extension (Pt. carnosa, Pt. biminiensis, Pt. jamaicensis, Sp. alba).
- 3. The end-sac may open into the medullary tube behind the anterior neuropore  $(Pt.\ carnosa)$ .

If, by a legitimate mental abstraction, we reflect upon the condition in which there is a coecal sac opening into the medullary tube which, in its turn, opens to the exterior by the neuropore, we have before us essentially the combination met with in the Ascidian larva with the difference that, in the latter, the neuropore does not open directly to the exterior but into the dorsally placed mouth.

<sup>&</sup>lt;sup>1</sup> The structure described by Masterman in a species of Actinotrocha as a neuropore is what Spengel would rightly call an "Epidermistasche," and is certainly not a neuropore in the strict sense. (A. T. Masterman, "On the Diplochorda," Q. J. M. S., Vol. 40, 1897, p. 281.)

<sup>&</sup>lt;sup>2</sup> Although paired water-pores have never been demonstrated to exist in Tornaria, they have been observed to have a normal though transitory existence in certain Echinoderm larvae, by Metschnikoff, Brooks, Field and Grave. (See Caswell Grave, "Embryology of Ophiocoma echinata Agassiz," *Johns Hopkins Univ. Circ.*, Vol. 18, Nov. 1898, p. 6.)

<sup>3</sup> By this term I shall, in the remarks which follow, refer to what Spengel calls the "Eichelpforte."

The theory, as to the broad truth of which I am myself quite convinced and for which I will proceed to produce the available evidence, may be stated briefly as follows:—
The proboscis pore¹ of the Enteropneusta is represented by and is homologous with the inner or cerebral opening of the neuro-hypophysial apparatus of the Ascidian larva; the end-sac of the Enteropneusta typically communicates internally with the coelom, but, within the limits of the group, we find signs of its emancipation² from the coelom; the hypophysial canal of the Ascidian larva has no relations with the body-cavity but it opens at one end into the medullary tube (cerebral vesicle) and at the other into the branchial sac at the base of the buccal cavity. Thus a special significance is given to the peculiar mode of origin of the Ascidian subneural apparatus (gland and duct) and an explanation is forthcoming as to the apparent absence of anything like a proboscis-pore in the Ascidian larva³.

a. Evidence of change of function; Excretory system of Enteropneusta. Apart from the evidence as to change of function, or loss of previous function of the proboscispores which is furnished by the fact of their greater or less emancipation from the coelom, there is also evidence of another kind. The proboscis-pores are clearly homodynamous with the collar-pores and the truncal pores (presumed vestiges of which occur in Spengelia). It is to be supposed that these three pairs of regional pores represent the primitive excretory canals of what Masterman (1897 loc. cit.) has called the archimeric regions of the body. But they no longer function as excretory canals since the function of excretion has been relegated to the glomerulus (proboscis-gland of Bateson) which is a structure sui generis. It might be supposed that the proboscispores would at least carry off the products of excretion resulting from the physiological activity of the glomerulus, and it is possible that this does occasionally happen. But if it were their essential function it should invariably happen. But it does not. In Bal. canadensis Spengel has found that the proboscis-pores are quite vestigial and in Pt. flava, as described above, the communication between the end-sacs and the proboscis coelom is sometimes occluded and sometimes quite obsolete.

It will be asked what becomes of the products of excretion if they are not discharged to the exterior, and the answer is that it is not absolutely necessary, in animals of the grade of organization of the Enteropneusta, that excretory products should be removed from the body (e.g. Ascidians). In close topographical relation with the glomerulus is a capacious vesicle closed on all sides, called the pericardium (Herzblase) on account of its relations to the central blood-space.

The endothelium of this so-called pericardium is subject to remarkable proliferation which varies greatly in its amount in different individuals (perhaps at different periods in one individual). It is quite reasonable to suppose that besides its topographical relations to the vascular complex known as the glomerulus it possesses functional relations with that organ. If this be so, the pericardium of the Enteropneusta in

<sup>1</sup> I say nothing as to dextral or sinistral pore or both.

<sup>&</sup>lt;sup>2</sup> Apropos see also Spengel on Bal. canadensis and Bal. kupfferi (Mon. pp. 472—473.)

<sup>&</sup>lt;sup>3</sup> Cf. A. Willey, "Studies on the Protochordata. II. The development of the neuro-hypophysial system in Ciona intestinalis and Clavelina lepadiformis." Q. J. M. S., Vol. 35, 1893, p. 295.

its capacity of closed vesicle associated with the renal function would be physiologically comparable to the **organ of Bojanus** of the Molgulidae<sup>1</sup>.

As for the collar-canals, since the essential organ of excretion is situated in the proboscis it is obvious that some function other than that of excretion must be assigned to them. Spengel gives good reason for supposing that the collar-canals serve for the ingress of sea-water into the collar-coelom for the purpose of procuring turgidity to assist in the peculiar method of locomotion of the Enteropneusta.

It is possible that this also takes place through the proboscis-pores in certain circumstances and in certain species. But whereas the function of the collar-canals, whatever it be, is constant, that of the proboscis end-sacs is as inconstant as they are variable. In all species examined by me the end-sacs of the proboscis taper considerably towards their internal (anterior) end. As we have seen, this tapering is sometimes carried so far as to obliterate the coelomic opening of the sac. The collar-canals maintain their calibre throughout their entire length and open invariably into the collar-coelom by a wide semilunar funnel.

It follows from what has preceded that both the proboscis-pores and collar-pores are vestigial in respect of their primitive excretory function, but whereas the latter have become definitely committed to an important and constant new function, the former are in a completely unsettled state. Their only hope lies in their capacity for forming new associations.

The proboscis-pores and collar-pores of the Enteropneusta considered as homodynamous structures may be contrasted as follows:—

PROBOSCIS-PORES.

Highly variable.

Coelomic opening reduced or absent.

Function impaired.

COLLAR-PORES.

Remarkably constant. Coelomic opening wide, semilunar and constant. Function true.

It is a matter of great importance to note the definite fact that a proboscis end-sac can persist as a coecal tube opening to the exterior after the loss of its coelomic opening. The very fact that the end-sac persists under such circumstances is surely evidence that its potentialities are not yet exhausted, and the outlook becomes still more encouraging if it can become associated with the neuropore and with the medullary tube. We have seen that this is a demonstrable possibility (cf. Pl. XXIX. Fig. 17 A).

Regional pore-canals can persist as vestiges after the loss of their coelomic openings. Such vestiges, by acquiring new associations, may resume their physiological activity in another sphere, by change of function; or, they may be entirely superseded by a new generation, i.e. by substitution, and so drag out the remainder of their existence in a condition of vestigial degeneration.

<sup>&</sup>lt;sup>1</sup> Spengel regards the anterior body-cavity (proboscis coelom) of Enteropneusta as an organ of the left side, its dextral antimere being represented by the pericardium (Herzblase) [Mon. p. 681 et seq.]. Such extraordinary complexity of structure and development as we have to deal with in the Enteropneusta is capable of being regarded from different points of view.

β. Historical. In 1881 Julin published, in the Archives de Biologie (T. II.), his well-known anatomical work on the subneural gland of Ascidians, in which he developed the idea that the subneural gland with its duct which opens dorsally into the branchial sac at the base of the buccal siphon by the dorsal tubercle, is homologous with the hypophysis cerebri of craniate Vertebrates. This work was followed in 1884 by a memoir published in the fifth volume of the same Archives under the joint names of Éd. van Beneden and C. Julin, in which the authors sought to substantiate their hypothesis by the facts of development.

They described the origin of the subneural gland in a species of *Clavelina*, from a simple evagination of the wall of the branchial sac, which they called the "caecum hypophysaire." This method of development is of course, in the main, like that followed by the hypophysis of the Craniota and would, if true, no doubt tend to support their hypothesis. It would at the same time rob the Ascidian subneural gland of any morphological interest that might be expected to appertain to it, because it would prove identity where we might reasonably hope to find evidence of change.

In 1892 (Zool. Anz. xv. 1892, p. 332) I showed that in Ciona intestinalis and Clavelina lepadiformis the adult ganglion and the subneural gland arise from a common primordium which I called the **neuro-hypophysial canal**. This canal opens primarily at its posterior end into the cerebral vesicle, while at its anterior end it secondarily acquires an opening (which may be defined as the rudiment of the dorsal tubercle) into the base of the dorsal mouth. There is good reason to interpret this secondary communication with the mouth as a re-opening of the neuropore. A similar mode of development has since been described in other forms by Hjort<sup>2</sup>, Salensky and Metcalf.

Meanwhile in 1886, Bateson<sup>3</sup> compared the proboscis-pore of *Balanoglossus* with the praeoral pit of the larva of *Amphioxus* and, on the strength of Julin's anatomical work, with the dorsal tubercle of the Ascidian subneural gland. Bateson's other suggestions on this point were of course made before the development of the subneural gland was known and need not be referred to here. In concluding his remarks on this subject he says (p. 564), "If these views are correct the pituitary body and its pore is to be regarded as the rudiment of a primitive excretory organ which originally opened dorsally." As will be seen, this conclusion is borne out by facts (see below, p. 314).

Strange as it may appear, it is nevertheless true that it has generally been found easier to compare the Urochorda with the Craniota than with the Enteropneusta, i.e. easier to compare them with higher than with more primitive forms.

The idea of the neuro-hypophysial canal does not appear to have gained many adherents, and it is no doubt very right that it should have been so until further information was forthcoming. This information is now to hand and it may be summed up by saying that the pore-canal or end-sac of the proboscis of Enteropneusta is homologous with the primordium of the subneural gland of Ascidians, this primordium being

<sup>&</sup>lt;sup>1</sup> The same suggestion was made in the same year by Balfour in his Comparative Embryology.

<sup>&</sup>lt;sup>2</sup> Hjort dealt with *Distaplia magnilarva*, and his preliminary account appeared at the same time as my own (Zool. Ans. xv. 1892, p. 328).

<sup>&</sup>lt;sup>3</sup> W. Bateson, "The Ancestry of the Chordata," Q. J. M. S., Vol. xxvi., 1886. See also Bateson's previous papers in the same and two preceding volumes.

the neuro-hypophysial canal; the proboscis-pore of Enteropneusta is represented in the Ascidian larva by the pore leading from the neuro-hypophysial canal into the cerebral vesicle; the anterior neuropore of Enteropneusta is represented in the Ascidian larva by the pore leading from the neuro-hypophysial canal into the mouth.

γ. Association of mouth and neuropore. We have already dealt with the association of proboscis-pore and neuropore. It now remains to say a few words on the association of mouth and neuropore in order to appreciate the comparison between the anterior trematic complex (mouth, neuropore and proboscis-pore) of the Enteropneusta and of the Ascidian tadpole.

For my part, when I say that the mouth of the Ascidian tadpole is dorsal and the mouth of the Enteropheusta is ventral, I mean that in one case the mouth is on one side of the body, and in the other it is on the opposite side of the body.

The comparison may be tabulated as follows:

### ENTEROPNEUSTA.

- 1. Mouth ventral.
- 2. Mouth a vast crescentic or sub-circular orifice facing forwards.
- 3. Mouth indirectly associated with neuropore in virtue of the projecting collar-flap (Pl. XXVII. Fig. 6 A).
- 4. Food ingested as the animal burrows through sand, vast quantities of which pass through the alimentary canal where the nutritious matter is extracted and the sand rejected.

### ASCIDIAN LARVA.

- 1. Mouth dorsal.
- 2. Mouth a minute circular orifice facing upwards.
- 3. Mouth directly associated with neuropore, the latter opening into the buccal cavity.
- 4. Doubtful if larva feeds at all; in many cases it certainly does not. If it does the food (as in adult) is ingested by ciliary currents and consists of micro-organisms and organic débris.

In the locomotion of the Enteropneusta the muscular proboscis is the essential organ of burrowing, and the distensible collar the essential organ of progression<sup>1</sup>.

The passage of the mouth from the ventral position which it occupies in the Enteropneusta to its dorsal position in the Ascidian larva may perhaps be attributed physiologically to the increased importance and efficiency of that association of mouth and neuropore which may be said to be already foreshadowed in the Enteropneusta (see Pl. XXVII. Fig. 6 A). The practical difficulty in the way of this translation of the mouth presented by the proboscis intervening between the latter and the dorsal surface can be supposed to have been, and probably was, surmounted pari passu with the change of function of the proboscis from a muscular burrowing organ to a non-muscular snout or fixing organ. This change would carry with it changes in the entire order of development and the mouth could open dorsally coincidently with the neuropore before the formation of the praeoral lobe. This is essentially what does happen<sup>2</sup>.

<sup>1</sup> A remarkably pretty analogous method of locomotion is exhibited by *Dentalium*, a species of which I had the opportunity of observing at Lifu. Here the muscular foot with its pointed end is the essential organ of burrowing, while the two lateral aliform lobes, which expand at the proper moment, together constitute the essential organ of progression.

<sup>2</sup> See A. Willey, "Studies on the Protochordata," I. Q. J. M. S., Vol. xxxv., p. 317 and III. Ibid. Vol. xxxv., p. 316. My interpretation of the organ of fixation of the Ascidian larva as praeoral lobe has been met with some natural scepticism, but on this point I may say that my views remain unchanged. As it happens, however, this is a point of detail, and we can go a long way without it.

It is perhaps not out of place to enquire whether there is any parallel instance of a minute, toothless, buccal orifice facing upwards. One of the most remarkable Teleostean fishes I have ever seen, namely, Amphisile strigata Guenther<sup>1</sup>, has the habit which I observed for the first time near Dawson Straits in the D'Entrecasteaux Group (British New Guinea), of swimming in an upright position in the water by means of its pectoral fins. The caudal and pelvic fins are vestigial. The entire ventral surface from tip to tail is as sharp as a knife-edge. The animal is pointed at both ends, about six inches long, one inch maximum height and \(\frac{1}{4}\)-inch maximum thickness along the back. It cuts through the water with its razor-edge at a great rate, and the mouth is an extraordinarily minute terminal toothless orifice pointing upwards in consequence of the erect swimming attitude.

## III. REGIONAL PORES AND NEPHRIC TUBULES.

Bateson was the first to compare the proboscis pore of Balanoglossus with the orifice of the praeoral pit of the larva of Amphioxus, basing the comparison upon Hatschek's account of the origin of the praeoral pit from the left division of the head-cavity. In view of the uniquely amphioxine nature of the origin of such a structure as the praeoral pit, combining the properties of gland and sense-organ, from a coelomic pouch; also in view of recent attempts to discredit Hatschek's discovery, a few general aspects of the question may be brought into view.

In the first place it is quite certain that one's morphological sense of coelomic propriety would never have been offended if the left head-cavity had acquired a communication with the exterior by means of a minute pore (which might perhaps have been difficult to find in section) instead of by a generous embouchure.

In the second place it is well to remember what seems to be usually forgotten, namely, that Hatschek's discovery was the result of unbiassed observation and no theoretical consequences were made to hang upon it until Bateson made the comparison referred to above.

Lastly Hatschek's account of the origin of the praeoral pit, which was based upon observations upon the living embryos, has recently been confirmed in section by MacBride<sup>2</sup>.

It is much easier to unravel the **anterior trematic complex** of the Ascidian larva than that of *Amphioxus*. In the larva of *Amphioxus* we have mouth, praeoral pit<sup>3</sup>, neuropore, and *Kölliker's olfactory pit* which arises as an epidermal depression over the neuropore. The olfactory pit is the disturbing element. The most obvious conclusion is that it is comparable with Spengel's anterior Epidermistasche in the Enteropneusta, but I do not think this is quite the right conclusion. Neither do I think that the comparison of the proboscis-pore with the orifice of the praeoral pit is as simple a matter

<sup>&</sup>lt;sup>1</sup> Kindly identified for me by Mr G. A. Boulenger, F.R.S.

<sup>&</sup>lt;sup>2</sup> E. W. MacBride, "The early development of Amphioxus," Q. J. M. S., Vol. xL., 1898, p. 589.

<sup>3</sup> The praeoral pit itself undergoes a certain amount of differentiation, but this does not directly concern us now.

as might appear. All these structures in animals of the grade of organisation of the Enteropneusta, Cephalochorda and Urochorda are in a more or less primordial condition, and hence appear deceptively simple just as an egg-cell which conceals the potentialities of the future organism may appear a simple matter.

In the Enteropneusta there are, as we have seen, dorsal canalicular portions of the proboscis coelom separated from one another by the pericardium. Each of these dorsal coelomic canals may, but usually only one does, open into a tubular end-sac, which in turn opens to the exterior. Bateson found in *Bal. kowalevskii* that the end-sac arises as an ectodermal ingrowth, and Spengel has found the same in regenerating specimens of *Pt. minuta*.

We have to consider therefore the possible and particular fate of

- 1. The dorsal coelomic canals in their capacity as portions of the proboscis coelom or anterior body-cavity.
- 2. The opening of a coelomic canal into an end-sac, which is equivalent to the opening of the coelom at an ectodermal surface.
  - 3. The end-sac itself.
  - 4. The external orifice of the end-sac.

With regard to the fate of the anterior body-cavity there is one remote though instructive ground of comparison between the Enteropneusta and the Cephalochorda. In the larva of Amphioxus the larger or dextral portion of the head-cavity (usually called the right head-cavity) forms the cavity of the snout or rostrum. In the adult this cavity is lost in the massive development of the laminar tissue (Pouchet) which is characteristic of Amphioxus. Similarly in the Enteropneusta the posterior ends of the coelomic canals of the proboscis lose themselves in and contribute cellular islets to, the chondroid tissue (Marion, Spengel).

It is very important to remember that in dealing with these structures there are two kinds of pores to be accounted for and not one pore only (above Nos. 2 and 4). In the path which has culminated in the Urochorda the coelomic opening (above No. 2) has, I believe, demonstrably vanished. It may not have vanished in Amphioxus; it may have had there another fate, a change of destiny instead of annihilation.

The praeoral pit of the larva of Amphioxus is a portion of the coelom which opens to the exterior, that is to say, which opens at an ectodermal surface. It has been the custom to speak of the right and left head-cavities of Amphioxus. This is correct in one sense, but in one sense only. Ontogeny teaches us (and this is borne out by comparative embryology) that the right and left head-cavities of Amphioxus are subdivisions of one anterior body-cavity, and are not paired structures in the same sense in which the collar-cavities are paired. The praeoral pit therefore should not be defined as the left head-cavity, but as the sinistral portion of the head-cavity which acquires independence and an opening to the exterior.

I therefore suggest that the orifice of the praeoral pit of the larva of Amphioxus represents the opening of the coelom into the end-sac of the Enteropneusta; the end-sac and its external orifice are represented in Amphioxus by Kölliker's olfactory pit which coincides in its point of origin with the pre-existing neuropore, which hence opens into its base<sup>1</sup>; the coelomic portion of the anterior trematic complex is therefore still existent in Amphioxus, but it is separated from its terminal portion (end-sac) concurrently with the forward extension of the notochord in the same way as the mouth has been dissociated from the neuropore<sup>2</sup>.

Hatschek described, as of mesodermal origin, a subchordal praeoral tube on the left side of the larva of Amphioxus. This has been called Hatschek's nephridium, and its opening into the anterior buccal portion of the pharynx was described and figured by Lankester and Willey<sup>3</sup>. MacBride (loc. cit.) has recently found that at an early stage this tube is in open primary communication with the somite which he has called the left collar-cavity, and in fact that it arises as a canalicular extension of the hollow stalk which connects the left collar-cavity with the archenteron. It only occurs in the larva, is lost during the metamorphosis, and is probably a vestigial structure.

The collar-canals of the Enteropneusta may be said to open into the pharynx through the mediation of the first gill-pouch and of the first gill-cleft (cf. Pl. XXXII. Fig. 52). The inference is obvious that Hatschek's nephridium is an unpaired vestige of the excretory canals of the collar region.

I have already (see pp. 273 and 280) compared the vestigial truncal canals of Spengelia with the atrio-coelomic funnels (Lankester) of Amphioxus.

<sup>1</sup> This is in complete accordance with the view which I have expressed on a former occasion, that Kolliker's olfactory pit represents the neuro-hypophysial canal of the Ascidian larva. By the epidermal invagination (at a late stage) which produces Kölliker's olfactory pit the neuropore is carried inwards at its base, and no longer opens flush with the surface of the body. In this way the neuropore acquires a new quality, namely, it becomes the cerebral opening of the olfactory pit or neuro-hypophysis. Thus in Amphioxus, the neuropore and the inner or cerebral opening of the neuro-hypophysis coincide. That there are two structures involved is indicated by the fact that the neuropore exists for a long time in the absence of a neuro-hypophysis (olfactory pit). As described by me in Ciona (loc. cit.) it appears that a large portion of the duct of the adult subneural gland is derived from a secondary evagination of the wall of the buccal siphon at the lips of the primary branchial or buccal orifice of the neuro-hypophysis (see Quart. Journ. Micro. Sci. Vol. xxxv. pp. 305-306). In this way the primary opening of the neuro-hypophysis into the mouth is carried inwards just as the neuropore in Amphioxus is carried inwards by the formation of Kölliker's olfactory pit. Thus the dorsal tubercle of the adult subneural gland is not the same thing as the primitive opening of the neurohypophysis, but it may be said to correspond with the external orifice of Kölliker's olfactory pit. The olfactory pit and neuropore in Amphioxus together represent the neuro-hypophysis of the Ascidian larva; the subneural gland of the adult Ascidian which develops from the neuro-hypophysis is not represented in Amphioxus and is, so far as we know, a purely Ascidian structure.

<sup>&</sup>lt;sup>2</sup> I offered an explanation of the dissociation of the larval mouth from the neuropore in 1891 (A. Willey, "The later larval development of Amphioxus," *Quart. Journ. Micro. Sci.*, Vol. xxxII., 1891), which has met with some favour.

<sup>&</sup>lt;sup>3</sup> E. Ray Lankester and A. Willey, "The development of the atrial chamber of Amphioxus," Quart. Journ. Micro. Sci., Vol. XXXI., 1890, p. 445.

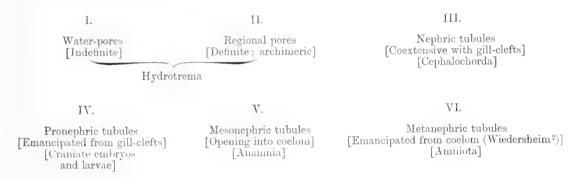
Thus, if the above comparisons are correct, *Amphioxus* possesses at some period of its life vestiges of the three pairs of regional or archimeric excretory canals, whose function has been superseded (by substitution) by the nephric tubules.

I have suggested above (p. 281) that the primordia of the nephric tubules may actually be recognised at the dorsal medial angles of the gill-pouches of Enteropneusta (cf. Pl. XXXII. Fig. 55 dqp).

In any case it is quite certain that the topographical coincidence of the nephric tubules with the gill-clefts as described by Weiss and Boveri in *Amphioxus* is not an accidental association. It evidently means what it appears to mean, namely, that the nephric tubules and the gill-clefts were primarily coextensive.

The nephric tubules of Amphioxus have superseded the regional pores as the essential organ of excretion but in a very different way from that in which the latter are superseded in the Enteropneusta by the glomerulus, which is an organ sui generis. The nephric tubules belong to the same cycle of changes as the regional pores and originate from the same blastema. They replace the regional pores by true substitution, just as in the Vertebrata the mesonephros replaces the pronephros and the metanephros the mesonephros.

Whether or not the regional pores arose as such or have been differentiated from a more indefinite condition as seen in the multiple madreporites of many Echinoderms is not an easy question to decide. The analogy with other cases would lead us to suppose that the ideal condition indicated in the adjoining table is not the primordial condition. We may at any rate formulate provisionally the following sequence of phyletic changes relating to the evolution of the Vertebrate kidney.



The following table expresses in brief the conclusions to which we have arrived, but it should be taken in conjunction with the text to avoid misunderstanding.

It is intended to show the origin, by substitution, of the Vertebrate excretory system from the archimeric system of excretory canals. Of course the table will only

<sup>&</sup>lt;sup>1</sup> By realising this truth, Paul Mayer's discovery of the six connecting vessels between dorsal aorta and subintestinal vein in embryos of *Prostiurus* and Rückert's discovery of their topographical coincidence with the pronephric tubules, to which they furnish rudimentary glomeruli, will have assigned to them the importance which is their due.

<sup>&</sup>lt;sup>2</sup> R. Wiedersheim, "Ueber die Entwicklung des Urogenitalapparates bei Crocodilen und Schildkröten," Arch. f. mikr. Anat., Bd. xxxvi., 1890, p. 410.

accomplish this object on the assumption that the nephric tubules of Amphioxus (i.e. as we know them in Amphioxus) represent the primordium of the Vertebrate kidney.

| GROUP                   |   | Archimeric <sup>1</sup> System |                              | Essential Organs of Excretion                       |
|-------------------------|---|--------------------------------|------------------------------|---|
| Ideal                   | Protomeric pores                              | Mesomeric pores                | Opisthomeric pores           | Regional pore-canals                                |
| Enteropneusta           | Proboscis pores                               | Collar pores                   | Truncal pores<br>(Spengelia) | Glomerulus  |
| Cephalochorda           | Praeoral pit +<br>olfactory pit               | Hatschek's<br>nephridium       | Lankester's<br>brown funnels | Boveri's nephric tubules                            |
| Urochorda               | Neuro-hypophysis<br>(in part <sup>3</sup> )   |                                |                              | Renal vesicles;<br>Organ of Bojanus<br>(Molgulidae) |
| Vertebrata <sup>2</sup> | Hypophysis<br>cerebri (in part <sup>3</sup> ) |                                |                              | Pronephros Mesonephros Metanephros                  |

<sup>&</sup>lt;sup>1</sup> In this table I have incorporated the terms archimeric, protomeric, &c. in the sense in which they were introduced by Masterman ("On the Diplochorda," Quart. Journ. Micro. Sci., Vol. 40, 1897, p. 281). He describes the tripartite division of the coelom as archimeric segmentation, and the three archimeres are (1) Protomere, (2) Mesomere, (3) Metamere. The last is inadmissible because metamere already has a meaning of its own, and I must therefore replace it, for my present purpose, by the term opisthomere.

<sup>&</sup>lt;sup>2</sup> In 1886 Bateson wrote:—"Upon the origin of the excretory system of Vertebrata nothing can be affirmed from a study of Balanoglossus." I trust the above table will illustrate the progress that has been made in this matter during the last ten or twelve years.

<sup>&</sup>lt;sup>3</sup> In part because coelomic element is wanting.

## IV. COLLAR NERVE-CORD AND ROOTS.

Spengel does not regard the collar nerve-cord of the Enteropneusta as the central nervous system but as being only a part of it which has become closed in. This is a highly important view, and it is again with satisfaction that I find myself in agreement with Spengel. He defines the collar nerve-cord (Mon. p. 705) as "die Einsenkung des auf den Kragen entfallenden Theiles des dorsalen Nervenstammes, der in seiner ganzen Länge vom Grunde der Eichel bis in die Nähe des Afters bereits vorher nicht nur angelegt, sondern in allen seinen charakteristischen Zügen ausgebildet ist."

The **centralisation** of the nervous system of the Enteropneusta has not proceeded far. There is concentration along the middle line on the dorsal or sensory side of the body and another concentration along the middle line on the ventral or locomotor side of the body. The dorsal concentration or dorsal nerve-cord of the trunk passes directly into the ventral wall of the medullary tube in the collar region and at the junction of medullary tube and dorsal cord, *i.e.* at the posterior edge of the collar a circular commissure passes round to unite with the anterior end of the ventral nerve-cord.

Bateson pointed out that the dorsal side of the medullary tube of the collar was the sensory side and received afferent fibres through the so-called dorsal roots or at the two ends of the cord in those forms which do not possess roots; and that the ventral side of the medullary tube from which efferent fibres pass into the muscles, is the motor side. The conclusion he came to was practically the only one possible at that time, namely, that the roots of the collar cord of Enteropneusta "are to be regarded as the homologues of the dorsal roots of other Chordata."

"In Balanoglossus<sup>2</sup>," says Bateson (1886 loc. cit. p. 558), "we see in the trunk the cord still in the skin, in the collar the cord delaminated<sup>3</sup>, and at the ends of this cord the process of invagination commencing and leading to the presence of a lumen."

This quotation shows that Bateson was alive to the fact that the collar cord is only a local differentiation of the dorsal cord as a whole. This fact is still more clearly expressed by Morgan (Journ. Morph. Vol. IX. 1894, see p. 74) in the following words, which I heartily endorse:—"We see in Balanoglossus that the invaginated dorsal nervecord can correspond only to the anterior end of the nerve-cord of Amphioxus, and that the superficial dorsal nerve-path, stretching through the gill region thence to the end of the body, must be the homologue of the remainder of the nerve-cord of Amphioxus."

<sup>&</sup>lt;sup>1</sup> The ingenious method of homologising the reverse sides of the body in Vertebrates and Invertebrates by employing the terms "neural" and "haemal" instead of "dorsal" and "ventral" is a gigantesque example of a petitio principii.

<sup>2</sup> That is to say Bal. kowalevskii.

<sup>&</sup>lt;sup>3</sup> In Bal. kowalerskii the collar nerve-cord arises in a peculiar manner akin to delamination. In Tornaria as shown by Morgan and in regenerating Ptychodera flava as shown on Plate XXVI. it arises by fusion of medullary folds.

Baldwin Spencer compared the eye of the Ascidian tadpole with the pineal eye, the most tangible point of resemblance being in the method of formation of the lens, the entire eye, lens and retina being of myelonic origin. This comparison may still hold good so far as it goes. But the full significance of the pineal eye can only be appreciated when we have traced its origin, or at least its affinity, to something which was not an eye at all but a far more generalised sensory apparatus.

Moreover the result of recent work<sup>1</sup> (Klinckowström, C. Hill, etc.) has been to show that the epiphysial complex is not a simple outgrowth from the roof of the primary fore-brain; there may be more than one outgrowth; there may even be more than one pineal eye with retina and lens complete.

Without going into greater detail, I may refer the reader back to my account of the roots in *Pt. flava* (p. 234), the intra-epidermal canals in *Pt. carnosa* (p. 252), and the vestigial root of *Sp. porosa* (p. 271).

I have described the remarkable terminal bulb of the vestigial root of Spengelia porosa (Pl. XXXI. Fig. 40) as being in a condition of mucoid degeneration. Whether or not there is any trace of pigment in life I cannot say. Very probably there is some kind of colouring matter. But we do not expect to find any great display of pigment in the Enteropneusta since they are burrowing creatures, living concealed from the light of the sun and belonging essentially to the marine cryptozoic fauna. If Sp. porosa lived an exposed life the terminal bulb would probably be in a condition of pigmentose degeneration.

An epiphysial structure like an enteropneustic root can be transformed into an epiphysial structure like a pineal eye by losing its primary function, passing through a condition of pigmentose degeneration (or at least developing pigment in its walls) and then being rejuvenated by the acquisition of a new function, the agent of the rejuvenescence being some form of natural selection.

We may therefore infer the following cycle of events:-

| I.                   | II.        | III.        | IV.       |
|----------------------|------------|-------------|-----------|
| Enteropneustic roots | Pigmentose | Pineal      | Epiphysis |
| (Ptychoderidae)      | condition  | eve or eyes | cerebri   |

I will now state with confidence the following proposition.

The medullary tube of the collar of Enteropneusta is the homologue of the cerebral vesicle only of Amphioxus and of the Ascidian tadpole and probably represents no more than the primary fore-brain<sup>2</sup> (thalamencephalon) of Craniota; the roots<sup>3</sup> of Ptychoderidae

<sup>&</sup>lt;sup>1</sup> A. Klinckowström, "Beiträge zur Kenntniss des Parietalauges," Zool. Jahrb. (Abth. f. Anat. u. Ont.) vii. 1894, p. 249; Charles Hill, "The epiphysis of Teleosts and Amia," Journ. Morph. ix. 1894, p. 237; W. A. Locy, "Contribution to the structure and development of the Vertebrate Head," Journ. Morph. xi. 1895; see remarks on the Pineal Sense-organs, p. 561 and bibliography; also A. Prenant, Éléments d'embryologie...des vertébrés, Vol. ii. p. 566 et seq., Paris, 1896.

<sup>&</sup>lt;sup>2</sup> Whether or not it contains elements of the mesencephalon need not be discussed here. The fundamental truth is that the primitive cerebral vesicle has been closed in phylogenetically in advance of the spinal cord, which meanwhile is represented by the dorsal nerve tract in the skin.

<sup>&</sup>lt;sup>3</sup> I have not considered the origin of these roots themselves. All the facts which are known (e.g. the appearance of a median neural crest in Pt. flava (above, p. 235); the median keel observed by Spengel in

are genetically related to the epiphysial complex of Craniota; in the crucial nuchal region of the Enteropneusta are therefore to be found not the actual but the nearest possible approximation to the actual primordia of the hypophysis cerebri and of the epiphysis cerebri of Craniota.

## V. GENITAL PLEURAE.

From the statements and quotations contained in the preceding section it will be seen that there is considerable consensus of opinion in regard to the definition of the collar nerve-cord as the closed-in anterior portion of the dorsal trunk.

Just as the medullary tube of the collar is admittedly an invaginated portion of the dorsal nerve-trunk so the medullary folds which arise and fuse to form the medullary tube are to be regarded as specialisations of the anterior portion of pleural folds which are retained in the Ptychoderidae as the genital pleurae<sup>1</sup>.

In the Craniota there are two principal methods of formation of the medullary tube, namely;—

- (1) By medullary folds as in Elasmobranchii, some Ganoids, Amphibia, Sauropsida and Mammalia;
- (2) By solid proliferation or delamination as in Cyclostomes, some Ganoids, and Teleostei.

In the Protochorda we find essentially the same two methods in a simplified form, namely;—

- (1) Medullary folds in Urochorda;
- (2) A peculiar epithelial delamination in Cephalochorda.

In the Enteropneusta, within the limits of the group itself we find the same two methods, namely;—

- (1) Medullary folds as in the Tornaria of Pt. biminiensis (Morgan<sup>2</sup>) and in regeneration of Pt. flava (above, p. 245);
  - (2) Delamination as in Bal. kowalevskii (Bateson).

young Pt. minuta; and the remarkable keel also described by Spengel in adult Bal. kowalevskii, etc.) can be brought into accordance with the following definition.

The median roots of the Enteropneusta have arisen as differentiations from the raphe produced by the fusion of the medullary folds over the cerebral portion of the dorsal nerve-cord to form the medullary tube of the collar. This definition is based on the facts of anatomy. According to Morgan's account of the development of the Bimini Tornaria (1894 loc. cit.) it is not borne out by the facts of development. Singularly enough it does seem to be borne out in a remarkable manner in regeneration, which often appears to point the way to a conception where ontogeny fails (see above, p. 246).

<sup>1</sup> Cf. section on Regeneration in Pt. flava, above, p. 245, and Figs. 5A-E on Pl. XXVI.

<sup>2</sup> This is all the more noteworthy because *Pt. biminiensis* (see above, p. 291) is one of those species whose medullary cord does not possess an axial canal in the adult. The method adopted in *Tornaria agassizii* as described and figured by Morgan is also the method of fusion of medullary folds, but by a strange fatality my friend characterises it as being "exactly the same way that the nerve chord of Amphioxus is formed" (T. H. Morgan, "The growth and metamorphosis of Tornaria," *Journ. Morph.*, Vol. v. 1891, see p. 422).

As is well known it is Gegenbaur's view that the method of delamination is more primitive than the method of fusion of medullary folds. There are others who hold the opposite view. By considering how far the one or the other view will lead him to an appreciation of the subject in hand, the reader may choose for himself between the two views. If he chooses the method of delamination, then he takes upon himself the onus of explaining the meaning of the central canal. For my part I pin my faith to the medullary folds because by their means I see my way to the application of the principle of change of function, and to an approximate conception of the meaning of the central canal.

That the genital pleurae are structures which are capable of undergoing change of function is shown by various indications; perhaps more than anything by the fact that they already serve at least two functions, namely, the supreme function of carrying the gonads and the secondary function of protecting the branchial complex. That they do serve the latter function is quite obvious in a form like *Pt. flava*, while in a form like *Pt. carnosa*, where it is less obvious, it is none the less indicated by their capacity of uniting together over the gill-area by a mucous junction (Pl. XXVII. Fig. 6).

The capacity for change of function is also strikingly exhibited at the anterior end of the genital pleurae in species of the subgenus *Tauroglossus*, where they converge towards one another dorsally in the region of the posterior neuropore and no longer contain gonads in this region (cf. Pl. XXXII. Fig. 61).

Spengel has drawn attention to the more ventral position of the gill-slits in *Amphioxus* as compared with their more dorsal position in the Enteropneusta, and naturally uses this as an argument in favour of his views. That there is a difference I gladly admit. A process of readjustment has been at work. The dorsal gill-pores of the Enteropneusta are not present in *Amphioxus*.

It is a truism to say that change of function of an organ is and must be accompanied by correlated changes of organisation.

To take the particular case under discussion as an example it may be said that the change of function by which the genital pleurae could become converted into medullary folds would be accompanied by their complete emancipation from the gonads and, sooner or later, by the abolition of the dorsal gill-pores<sup>2</sup>, the gill-clefts finding another (ventral) outlet.

Analogous changes have apparently actually taken place in the collar; this is seen in cases of regeneration and may also be inferred on other grounds (see below p. 321).

It now becomes necessary to discuss the organisation of Amphioxus in the light of the above considerations.

We have seen that the pleural folds of the Ptychoderidae possess gonadial, medullary and peribranchial qualities. Taken as a whole therefore they constitute, potentially, a **complex primordium**. We have already dealt with their gonadial and medullary attributes and it only remains to consider their peribranchial potentialities.

<sup>&</sup>lt;sup>1</sup> Compare the excessive readjustment of the gill-clefts which takes place in the ontogeny of Amphioxus.

<sup>&</sup>lt;sup>2</sup> There are two ways of abolishing inconvenient gill-openings, namely, (1) by closure of the slits, (2) by realigustment of the slits. Both these methods are adopted in the larva of Amphioxus.

It is a subject of great complexity, and I can only indicate some of the facts and arguments which must be brought to bear upon it.

- 1. In virtue of their medullary and peribranchial properties, the pleural folds which are represented in the Enteropneusta by the genital pleurae must contain within them the primordia not only of medullary folds, but also of atrial folds.
- 2. Although Amphioxus is not the only animal which possesses an atrium, it is the only animal in which the atrium is formed by the fusion of atrial (metapleural) folds.
- 3. Amphioxus possesses atrial folds, but not medullary folds 1, the central nervous system forming cenogenetically by delamination.
  - 4. The two halves of the Tunicate atrium are confluent dorsally.
  - 5. The two halves of the atrium of Amphioxus are confluent ventrally.
- 6. The atriopore of Amphioxus is a neoformation. It is neither an orifice of invagination nor does it arise ontogenetically as a perforation of the body-wall, but it is a foramen remaining after fusion of folds.
- 7. Several species of the subgenus *Tauroglossus* are characterised by the presence of deep ventral coecal prolongations of the gill-pouches (*Pt. carnosa*, etc.).
- 8. In describing the condition met with in Amphioxus in terms derived from the comparison of Amphioxus with a form like Pt. carnosa, we should say that in Amphioxus the dorsal gill-pores are lost, the gill-pouches of each side are confluent longitudinally, and the gill-pouches of both sides are confluent ventrally, while the atriopore is a neoformation.
- 9. In order to appreciate the condition met with in a form like *Pt. carnosa* as compared with *Pt. flava*, a glance at Pl. XXX. Fig. 22, will show that if the septal walls dividing the successive gill-pouches from one another were to break down, so that the gill-pouches of each side became confluent longitudinally, we should have absolutely the condition which we actually find in *Pt. flava* (Pl. XXVIII. Fig. 6).
- 10. The ventral coeca of the gill-pouches of *Pt. carnosa* and other species are reminiscent of the ventral origin of the genital pleurae (compare Pl. XXX. Fig. 22, and Pl. XXVIII. Fig. 6).
- 11. Apart from the implication contained in the preceding hypothesis (No. 10), there is every reason to regard Pt. flava as a relatively primitive form.
- 12. Hence the gill-pouches of the Enteropneusta are structures superadded to the primitive organisation.

The broad generalisation which may be formulated as the summation of the preceding considerations is that the genital folds of Enteropneusta, the atrial folds of Amphioxus, and the medullary folds of Vertebrata belong to the system of pleural folds of the body-wall, and are differentiations from a common primordium.

#### VI. POSTERIOR TREMATIC COMPLEX.

I have already dealt with what I have called the anterior trematic complex (above, p. 309).

The **posterior trematic complex** of the Enteropneusta is situated at the posterior end of the collar in the dorsal middle line, and owes its existence to the close association of the posterior neuropore, the collar-pores, and the first pair of gill-pores<sup>1</sup>. It is unnecessary to repeat what has already been said in the account given of *Pt. carnosa* (see p. 253 and Pl. XXX. Fig. 21) and *Sp. alba* (see p. 280).

It is, however, very important to recognise the existence of the posterior trematic complex, the position of which in the Enteropneusta is due to the fact that only the cerebral portion of the central nervous system has been closed in as a medullary tube. Therefore while the mouth has relations with and forms part of the anterior trematic complex, the anus has nothing to do with the posterior trematic complex of the Enteropneusta.

As more of the cerebro-spinal axis becomes closed in by the fusion of the medullary folds, the association of pores which primarily constitutes the posterior trematic complex will be dissolved. When the fusion of the medullary folds reaches the anal region, the posterior trematic complex will comprise the association of posterior neuropore and blastopore (primitive anus).

We find here therefore a clue to the meaning of the neurenteric canal, which is due to the association of posterior neuropore and blastopore, and their inclusion within the medullary folds.

If there is any truth in what has been said, it is a matter of such importance that it may be stated categorically that the association of posterior neuropore and blastopore which generally leads to the formation of a neurenteric canal, is the posterior trematic complex of the embryos of Vertebrata.

#### VII. STOMOCHORD AND PYGOCHORD.

The presence of these skeletal products of the gut wall is undoubtedly an expression of the chordate strain in the Enteropneusta, but neither the one nor the other can be homologised with the notochord of the Vertebrata. The pygochord being ventral does not burden the question, but the stomochord is quite another matter. Although there is no question of the pygochord being compared directly with the notochord, yet I think it can be made very suggestive in any attempt to explain the latter.

The position of the stomochord has been compared with the forward extension of the notochord in *Amphioxus*. I am convinced that this comparison cannot be wholly sustained because the post-cerebral limitation of the notochord as seen in the Urochorda is undoubtedly more primitive than the cephalochordate condition of *Amphioxus*. Nevertheless, both in *Amphioxus* and in the embryos of Craniota there is frequently found a disturbance of some kind at the anterior end of the notochord, and this may be due to a local reminiscence of a stomochord.

<sup>&</sup>lt;sup>1</sup> To these must be added, in Spengelia, the truncal pores.

I doubt whether the enteropneustic stomochord as a whole can be said to correspond to any definite part of the true notochord. The praeoral extension of the notochord, far beyond the anterior limit of the neural tube in  $Amphioxus^1$ , is due to a forward growth of the pre-existing notochord; whereas the praeoral position of the stomochord in the Enteropneusta is due to a forward projection of a portion of the collar-gut or throat. Spengel calls it the "Eicheldarm," but this word, although intended to be indifferent, is apt to mislead, because the stomochord does not belong to the proboscis at all in its primary quality of integral constituent of the gut, but only in its secondary quality of a skeletally metamorphosed derivative of the gut.

Moreover, whereas the notochord is a uniform, single, indivisible structure, the regional differentiation of the stomochord is, as we have seen, one of its most marked characteristics. It is therefore not sufficient to say that any structure in other forms is comparable to the enteropneustic stomochord, but it must be specified which portion of this structure is referred to.

The cavity of the stomochord is in an obviously vestigial condition. In the days of its functional activity it must have been a portion of the post-oral gut cavity. Its secondary projection in front of the mouth is a fact which can only be explained at present by assuming a precocious segregation of its primordia, such a segregation being indicated by the fact of its developing from an apparently simple rudiment<sup>2</sup>.

As I have dealt with this matter in an article which will shortly appear in the Quarterly Journal of Microscopical Science, I can briefly state the conclusions to which I have come.

- 1. The "notochord" of Cephalodiscus is related to the vermiform process of the stomochord of Enteropneusta (Spengelidae). This was first suggested by Harmer<sup>3</sup>.
- 2. The pleurochords described by Masterman in the Actinotrocha of the Bay of St Andrews appear to be vestiges of gill-clefts which still persist in Cephalodiscus. These pleurochords occur in the lophophoral (collar) region of the body.
- 3. The pleurochords of Masterman are related to the lateral pouches of the stomochord of Enteropneusta.
- 4. Thus the lateral pouches of the stomochord may represent the vestiges of a pair of post-oral, but prae-truncal, gill-clefts; gill-clefts having been abolished from

<sup>1</sup> It is this extension of the notochord in front of the cerebral vesicle and neuropore which distinguishes the cephalochordate nature of Amphioxus from the holochordate nature of the Craniota.

<sup>2</sup> The terms rudiment and primordium are not capable of rigid definition and they are often interchangeable. The rudiment of a new organ is often the vestige of an ancient one, an old vestige becoming transformed into a new rudiment by substitution and change of function. In such cases therefore rudiment is the converse of vestige. Primordium is an independent term, and whereas every primordium is a rudiment, every rudiment is not a primordium. Of course no line of demarcation can be drawn between primordium and rudiment, nor can any be drawn between embryo and larva. The primordium of an organ is to the rudiment of an organ what the embryo of an organism is to the larval organism.

Mr G. C. Bourne at the meeting of the British Association in Bristol last year, pointed out that the word primordium, in the essential sense in which it is used in the text, originated with William Harvey.

<sup>3</sup> S. F. Harmer, "On the Notochord of Cephalodiscus," Zool. Anz. 1897, p. 342.

4 A. T. Masterman, "On the further anatomy and the budding processes of Cephalodiscus dodecalophus,"

Trans. Roy. Soc. Edin., Vol. xxxix. 1898, p. 507.

the collar region in the Enteropneusta and restricted to the truncal region in correlation with the regional differentiation of the body, and, connected therewith, the limitation of the gill-clefts (above, p. 298)<sup>1</sup>.

- 5. The ventral coecum with chordoid walls described by Roule (Comptes Rendus, t. CXXVII., 1898, p. 633) in the Actinotrocha of Phoronis sabatieri is related to the ventral coecum of the stomochord of Enteropneusta.
- 6. The functional oesophagus of Actinotrocha is represented by the anterior portion of the body of the stomochord in Enteropneusta.
- 7. Thus Actinotrocha and Cephalodiscus appear to retain in a functional condition a portion of the gut which in the Enteropneusta has become, as such, vestigial. That sessile forms should retain some primitive features in comparison with their free-living relatives is not without precedent.

The Pterobranchia are to the Enteropneusta what the Ascidians are to Amphioxus.

Apart from its ventral position, the pygochord seems to me to represent what must have been the condition of the notochord at its first inception; namely, the notochord was at first a longitudinal dorsal band-like thickening of the gut-wall with dilated distal border; and the subnotochordal rod represents the longitudinal peduncle of the longitudinal notochord. This explanation of the subnotochordal rod was suggested to me by the behaviour of the pygochord with its constrictions (cf. Pl. XXIX. Fig. 15 and Pl. XXX. Fig. 35), and it is, I think, the third explanation which has been suggested in recent years.

Stöhr<sup>2</sup> thought that the hypochorda resulted from the fusion of segmental diverticula of the dorsal wall of the intestine. Klaatsch<sup>3</sup> thinks that the hypochorda is the vestige of the hyperpharyngeal groove of *Amphioxus*<sup>4</sup>.

#### VIII. BRANCHIAL BARS.

One of the organic changes which accompanied the (hypothetical) change of function of the gill-clefts (i.e. from their primary function of promoting intergonadial currents of water to aerate the gonads to their secondary function of promoting the respiration of the individual) was the development of tongue-bars as the essential organs of respiration. It has already been pointed out that the tongue-bars of Enteropneusta are not (ontogenetically) secondary as they are in *Amphioxus*.

- ¹ The gill-clefts have been limited both anteriorly and posteriorly. The anterior limitation, behind the collar-region, is constant in all Enteropneusta; the posterior limitation is, as we have seen, excessively variable. In connection with the hypothesis that the lateral pouches of the stomochord are the vestiges of a pair of collar gill-clefts, it is useful to remember that in the larva of Amphioxus, the first gill-cleft does actually close up and disappear.
- <sup>2</sup> Ph. Stöhr, "Ueber die Entwicklung der Hypochorda und des dorsalen Pankreas bei Rana temporaria," Morph. Jahr. xxiii. 1895, p. 123.
- <sup>3</sup> H. Klaatsch, "Zur Frage nach der morphologischen Bedeutung der Hypochorda," *Ibid.* xxv. 1898, p. 156.

  <sup>4</sup> According to my view the absence of a subnotochordal rod in *Amphioxus* is due to abbreviation of development, *i.e.* it is a cenogenetic loss like the absence of medullary folds, etc. It may be remembered that Eisig compared the subnotochordal rod with the "Nebendarm" of Capitellidae.

By their development, size and vascularity, the tongue-bars of the Enteropneusta obviously constitute, collectively, the essential organ of respiration. In Amphioxus the functional importance of the tongue-bars is greatly diminished; they are smaller in size and lower in vascularity than the primary bars and their development is secondary. In Amphioxus therefore the conditions are reversed, the primary or septal bars constituting, collectively, the essential organ of respiration.

In correlation with the further reduction in the number of gill-clefts and the incorporation of the few that remain into the cephalic complex of craniate Vertebrates, the nephric tubules have been released from the topographical relation which they bear to the gill-clefts and to the tongue-bars in *Amphioxus*, and the tongue-bars themselves have disappeared as such. As I have suggested on a former occasion there is reason to believe that the tongue-bars have not vanished without leaving a trace behind, but that their degradation from the position of essential organ of the gill-cleft has culminated in their transformation into the primordial elements of the thymus of Vertebrata. The substance of the tongue-bars has been employed in building up the thymus.

The cycle of phyletic changes undergone by the tongue-bars of the gill-clefts may be epitomised as follows:—

| I.               | II.             | III.                  | IV.              |
|------------------|-----------------|-----------------------|------------------|
| Essential Organs | SECONDARY BARS  | VESTIGES              | THYMUS           |
| (Enteropneusta)  | $(Amphioxus_j)$ | (Embryos of Craniota) | (Adult Craniota) |

#### IX. PARABRANCHIAL RIDGES.

In the larva of Amphioxus the endostyle is seen to be composed of two halves, right and left<sup>2</sup>. From the anterior ends of the horns of the endostyle a pair of sharply defined ciliated bands—the peripharyngeal bands—arch round the anterior wall of the pharynx until they reach the dorsal side of the latter, whence they proceed backwards to the end of the branchial region. In the adult the dorsal pharyngeal wall becomes modified into the hyperpharyngeal groove and the ciliated bands merge into the walls of this groove. In the adult therefore it is impossible in surface view to see the dorsal recurrent portion of the bands, but it is, at least in young adults, eminently possible to see the anterior arcuate peripharyngeal portion of the ciliated bands<sup>2</sup>.

The parabranchial ridges (oesophageale Grenzwülste) of the Enteropneusta are likewise ciliated tracts (without the histological differentiation observed in the endostyle) which lie at the base of the gill-clefts and arch round in front to unite in the epibranchial band (Pl. XXVIII. Fig. 1 A and Text-fig. 7).

<sup>&</sup>lt;sup>1</sup> A. Willey, Amphioxus and the ancestry of the Vertebrates, 1894, p. 29. Cf. also Pierre de Meuron, Recherches sur le développement du Thymus et de la glande Thyroïde. Dissertation. Geneva, 1886. De Meuron gives some admirable diagrams to elucidate the origin of the thymus in different Vertebrata.

<sup>&</sup>lt;sup>2</sup> At first upper and lower owing to the peculiar configuration of the larva.

<sup>3</sup> In preserved specimens the contraction of the body quite obscures the ciliated bands in ninety-nine cases out of a hundred.

The change of function which would be associated with the transformation of the relatively undifferentiated parabranchial ridges into such a highly specialised organ as the endostyle is not easy to define<sup>1</sup>, and I limit myself to pointing out the similarity in topographical relations.

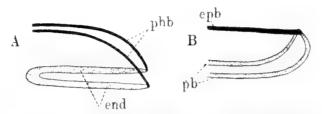


Fig. 7. Diagrams to illustrate the comparison of the specialised ciliated tracts in the pharynx of Amphioxus (A) and Enteropheusta (B).

end Endostyle. phb Peripharyngeal bands. pb Parabranchial ridges. epb Epibranchial band.

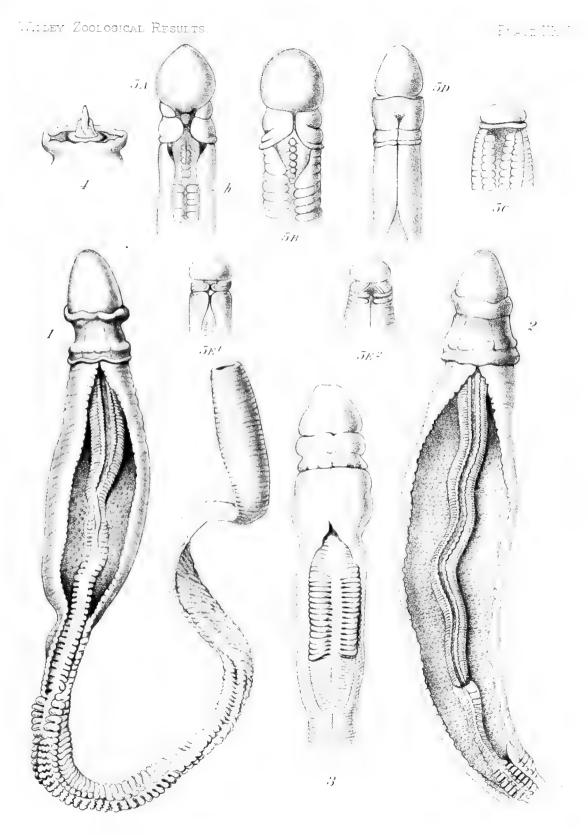
It is satisfactory to know that there exists something in the Enteropneusta which may be related to the endostyle but which nevertheless is not one.

The phyletic series of changes relating to the endostyle may therefore be tabulated as follows:—

| I.                   | II.                           | III.         |
|----------------------|-------------------------------|--------------|
| Parabranchial ridges | ENDOSTYLE                     | THYROID      |
| (Enteropneusta)      | (Cephalochorda and Urochorda) | (Vertebrata) |

<sup>1</sup> Of course it would be connected with changes in the entire habit of life, method of feeding, and quality of food.

Zoological Laboratory, New Museums, Cambridge, May 1st, 1899.



Zia · A · .. \* Cambridge

# EXPLANATION OF PLATES XXVI-XXXII.

The material was chiefly preserved in Mayer's Picro-Nitric solution and in a Chrome-Osmic mixture which was recommended to me specially for preserving Enteropneusta by Mr J. P. Hill. It gave excellent results and is the most reliable fluid for unique specimens. The following proportions are employed:—

Chromic Acid  $1^{\circ}/_{\circ}$ —100 c.c. Osmic Acid  $1^{\circ}/_{\circ}$ —2 c.c.

Objects may be left in this fluid for 12 hours (overnight) and then washed out in water. Specimens preserved in  $4-5^{\circ}/_{\circ}$  formalin are useful for dissection.

## REFERENCE LETTERS.

| a.    | Artefact.   | $qp^1$ . | First gill-pouch.                                  |
|-------|---|----------|--|
| adv.  | Advehent dermal vessel of proboscis.                | apc.     | Coecum of gill-pouch.                              |
| ag.   | Accessory gonads.                                   | gs.      | Gill-slit.   |
| an.   | Anterior neuropore.                                 | 481.     | First gill-slit.                                   |
| b.    | Blood-space.  | h.       | Pericardium (not in Pl. XXVI, Fig. 5A, q.v.)       |
| bm.   | Basement membrane.                                  | hq.      | Hind-gut.  |
| br.   | Branchial sac.                                      | i.       | Intestine.   |
| bs.   | Central blood sinus.                                | ic.      | Inner circular muscles of collar.                  |
| c.    | Collar coelom.                                      | ive.     | Intra-epidermal canal.                             |
| ca.   | Ciliated apparatus (ciliated grooves of intestine). | ıl.      | Inner longitudinal muscles of collar.              |
| cc.   | Collar canal.                                       | l.       | Hepatic saccule.                                   |
| cf.   | Collar funnel.                                      | la.      | Lateral gonad.                                     |
| cm.   | Circular muscles.                                   | lm.      | Longitudinal muscles.                              |
| cp.   | Collar pore.  | lp.      | Left proboscis pore.                               |
| ct.   | Fold in wall of collar canal.                       | lps.     | Lateral pouch of stomochord.                       |
| dgp.  | Dorsal diverticulum of gill-pouch.                  | ls.      | Lateral septum.                                    |
| dn.   | Dorsal nerve-cord.                                  | lv.      | Lateral vessel.                                    |
| dp.   | Dermal pit.   | mc.      | Medullary canal or cord (collar nerve-cord).       |
| drv.  | Dorsal recurrent dermal vessel of proboscis.        | mg.      | Medial gonad.                                      |
| ds.   | Dorsal septum (Mesentery in Pl. xxx. Fig. 32).      | ms.      | Median septum of proboscis.                        |
| dv.   | Dorsal vessel.                                      | ue.      | Outer circular muscles of collar.                  |
| ei.   | Epidermal involution.                               | oe.      | Oesophagus.  |
| ep.   | Epidermis.  | ol.      | Outer longitudinal muscles of collar.              |
| epb.  | Epibranchial tract.                                 | p.       | Proboscis coelom.                                  |
| ep.e  | Outer and inner epidermis of collar-flap.           | pb.      | Parabranchial ridge.                               |
| ep.i. | Outer and inner epidermis of contar-nap.            | pbc.     | Postbranchial canal.                               |
| ept.  | Epidermal tract.                                    | pc.      | End-vesicle or end-sac of proboscis (Eichelpforte) |
| et.   | Anterior epidermal involution (Epidermistasche).    | ph.      | Perihaemal cavity.                                 |
| ev.   | Efferent vessels of proboscis.                      | pnp.     | Posterior neuropore.                               |
| g.    | Gonads.   | pph.     | Peripharyngeal cavity.                             |
| gd.   | Genital duct.                                       | ptv.     | Post-trematic portion of end-sac (also pc.).       |
| gl.   | Glomerulus.   | py.      | Pygochord.   |

r. Root.

rf. Vascular ring of collar (Ringfalte).

rp. Right proboscis pore.

s. Stomochord.

sb. Septal bar.

sk1. Nuchal skeleton.

sk2. Chondroid tissue.

sp. Splanchnotheca.

t. Truncal coelom.

th. Tongue-bar.

tc. Truncal canal.

th. Throat and wall of throat (collar-gut).

tm. Transverse muscles.

vc. Ventral coelomic canals and coecum of proboscis.

vn. Ventral nerve-cord.

vp. Vermiform process of stomochord.

vrv. Ventral recurrent dermal vessel of proboscis.

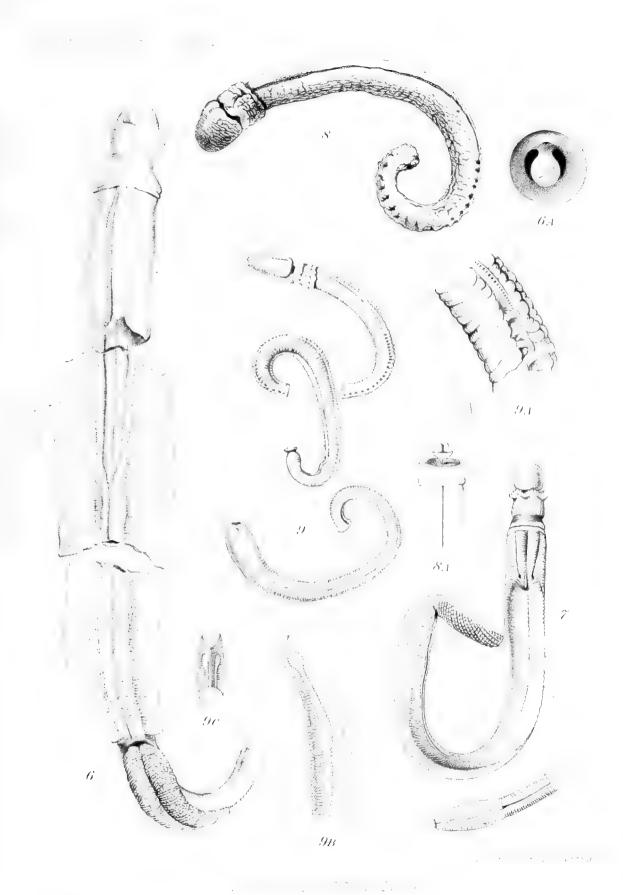
vs. Ventral septum.

vv. Ventral vessel.

## PLATE XXVI.

All the figures on this plate refer to Pt. flava.

- Fig. 1. Dorsal view of normal specimen with genital pleurae divaricated and exposing the free pharynx.  $\times$  3.
- Fig. 2. Similar view of anterior portion of macrobranchiate variety with fully expanded genital pleurae. The oval bodies disposed in zones on the inner surface of the genital pleurae are glandular dermal islets. × 3.
- Fig. 3. Similar view of brachybranchiate variety. The genital pleurae are closely approximated in the branchial region so as to cover in the pharynx. The hepatic tract is sharply defined, the saccules being arranged like the leaves of a book.  $\times$  6.
- Fig. 4. Anterior end of specimen from which the whole of the pre-nuchal region of the proboscis had been removed, showing the central complex projecting freely as a rigid body, hard to the touch. × 3.
- Fig. 5 A—E. The anterior ends of a series of regenerating individuals from the dorsal side (except  $E^2$ ).
- A. The medullary folds are wide apart, exposing the base of the collar nerve-cord throughout its entire length. The triangular body seen at the base of the collar groove in its anterior half is due to the vaulted floor of the groove (cf. Pl. XXXII. Fig. 66). The hepatic saccules commence at h and the entire pre-hepatic portion of the specimen measured 3.25 mm. in length.
- B. The medullary folds are still open but closely approximated. At the anterior end they are fused (see Pl. XXXII. Fig. 68). Proboscis + collar = 3.5 mm.
- C. A rudimentary proboscis and collar have been added immediately in front of the hepatic region.  $\times$  about 4.
- D. The medullary folds have completely closed over the collar nerve-cord, but there remains a deep dermal groove in the posterior half of the collar in the middle line. × about 3.
- $E^1$  and  $E^2$ . A regenerating individual from dorsal and ventral aspects to demonstrate the homodynamy of the zones of the collar with the annulations of the trunk.  $\times$  about 4.



#### PLATE XXVII.

- Fig. 6. Dorsal view of *Pt. carnosa* n. sp. to the end of the hepatic region; abdominal and caudal regions omitted. From preserved specimen, natural size. In front of the first fracture the genital pleurae are united together across the middle line by a mucous junction.
- Fig. 6.4. Frontal view of the head of *Pt. carnosa*. There is a scar across the small proboscis which probably indicates that the latter was recovering from an injury. The anterior neuropore is indicated in the dorsal angle made by the junction of the proboscis and collar, and below this are seen the lateral portions of the large buccal orifice.
- Fig. 7. Pt. ruficollis, n. sp. The hepatic region is denoted by the diagonal markings which commence shortly behind the termination of the genital ridges. The posterior end of the body is represented in ventral view to show the transition from the abdominal to the caudal region.  $\times 2$ .
- Fig. 8. Spengelia porosa in lateral view. From a photograph (x about 2) taken by Mr Grant in the Physiological Laboratory at the University, Sydney, N.S.W.
- Fig. 8 A. Sp. porosa. Ventral view of anterior end of macerated specimen showing the cupule and keel of the nuchal skeleton; the two horns of the glomerulus and the vermiform process of the stomochord projecting into the proboscis.
- Fig. 9. Sp. alba, n. sp. The entire animal in three fragments; the dotted lines show where the fragments should join on to one another.  $\times 1\frac{1}{2}$ .
  - Fig. 9 A. Sp. alba. Enlarged view of branchiogenital transition. × 6.
- Fig. 9 B. Sp. alba. Enlarged view of genito-hepatic transition and portion of hepatic region, to show smooth ventro-lateral epidermal tract. The dark line showing through in the posterior part of the drawing is due to the lateral blood-vessel of the hepatic region. The asterisk marks the corresponding points in Figs. 9 and 9 B.
- Fig. 9 C. Sp. alba. Ventral view of genito-hepatic transition to show the dilated ends of the ventro-lateral epidermal tracts.

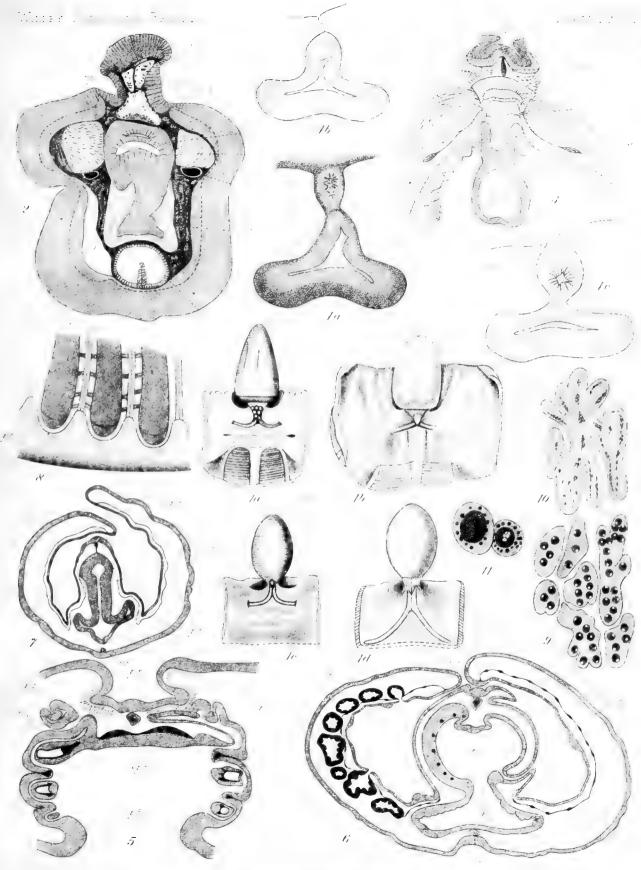
#### PLATE XXVIII.

- Fig. 1 a. Pt. flava. Collar and anterior end of pharynx opened up by a ventral incision. It shows the parabranchial ridges passing round into the epibranchial tract; also the racemose organ underlying the body of the nuchal skeleton immediately in front of the divaricating cornua of the skeleton. The lobulation of the racemose organ varies greatly in extent, the condition here represented being somewhat beyond the average.
- Fig. 1 b. Pt. carnosa. Similar view. Collar-flap projects far in front of insertion of proboscis; an epithelial pad underlies the nuchal skeleton in front of and below the point of bifurcation (cf. Pl. XXIX, Fig. 18).

- Fig. 1c. Pt. ruficollis. Collar opened by ventral incision. The projecting knob at the base of the proboscis is formed by the ventral coecum of the proboscis like the racemose organ in Pt. flava.
- Fig. 1 d. Sp. porosa. Similar view of macerated specimen. The alary processes and keel of nuchal skeleton are seen as well as the cornua of the skeleton reaching beyond the middle of the collar nearly to its posterior margin.

The remaining figures on this plate refer to Pt. flava; all sections are transverse unless otherwise stated.

- Fig. 2. Section through base of proboscis at the level of the proboscis-pores. The unequal size and wide openings of the pores may be noted. The section involves the free edge of the ventral septum of the proboscis, and the cupule of the nuchal skeleton. The dotted line in the epidermis indicates the line of demarcation between the nucleated and fibrous (nervous) layers of the epidermis.
- Fig. 3. Portion of section through the region of insertion of proboscis into collar, passing through the anterior neuropore. In this specimen the racemose organ (v.c) was slightly lobulated.
- Fig. 4 a—c. Sections through collar nerve-cord (medullary tube) showing central canal and hollow roots.
- Fig. 4a shows the first root meeting the epidermis and the basal crest from which it arises.
  - Fig. 4b shows the hollow neural crest between the first and second roots.
- Fig. 4c shows the second root arising by constriction from the neural crest and meeting the basement membrane of the epidermis.
- Fig. 5. Portion of section through the region of transition from collar to trunk, passing through the posterior neuropore (below which the dorsal vessel is seen); a collar-canal on the left and a collar-pore on the right, opening into the first gill-pouch.
- Fig. 6. Section through the branchial region showing genital pleurae and lateral septa. The gonads have been omitted from one side in order to show the lateral septum (which is perforated by the genital ducts) more clearly. A tongue-bar is shown on the right side of the figure, and a septal bar with cut ends of synapticula on the left side.
- Fig. 7. Section through the branchiogenital transition shortly behind the terminal gill-slits, showing the postbranchial canal.
- Fig. 8. Inner view of the basal portions of three gill-slits. Reduced from the *Quart. Journ. Micr. Sci.*, Vol. 40, Pl. 5, Fig. 3; it shows the wide tongue-bars and narrow septal bars united by synapticula or cross-bars.
- Fig. 9. A group of gonads containing ova as seen in situ in the genital pleura. (1bid. Pl. 5, Fig. 5.)
  - Fig. 10. Similar view of a single male gonad (Ibid. Fig. 4a.)
- Fig. 11. Nutritive bodies from gonads with darkly stained inclusions. The central body of the smaller cell shows refringent contents. Zeiss Oc. 3, Obj. J, water imm.

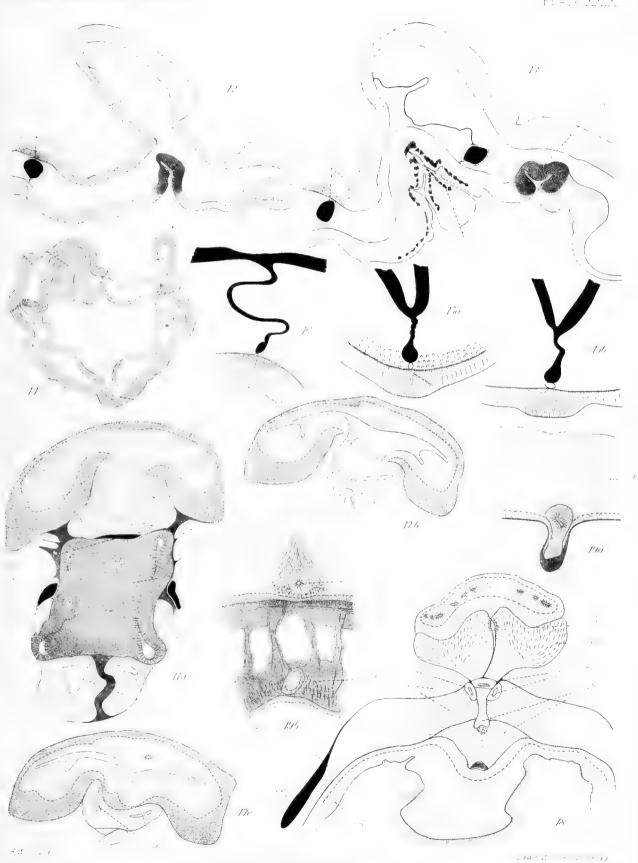


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## PLATE XXIX.

Figs. 12-15 refer to Pt. flavo.

- Fig. 12. Portion of section through hepatic region passing through an intersaccular interval showing sacculation of ciliated groove of intestine.
  - Fig. 13. Similar section passing through a liver-saccule.
- Fig. 14. Entire section through hepatic region involving a liver-saccule on the left and an intersaccular interval on the right.
- Fig. 15 a—b. Ventral portions of sections through caudal region to show the pygochord in its moniliform and simple aspects. The dilated ventral border of the pygochord abuts upon the ventral vessel.

Figs. 16--19 refer to Pt. carnosa, n. sp.

- Fig. 16. Ventral portion of section through caudal region to show the narrow lamelliform pygochord.
- Fig. 17 a—c. Portions of sections through the region of insertion of proboscis into collar, involving the posterior part of the proboscis end-sac (Eichelpforte).
- Fig. 17 a. Shortly behind the anterior neuropore, showing the end-sac lying below the medullary tube. The lumen seen in the ventral wall of the end-sac is a diverticulum from the main lumen. The body lying inside the sac is a tangential section through the duplicature of the wall of the sac, described in the text. The section passes through the middle of the coecal or pouched region of the stomochord; above the ventro-lateral pouches are seen the forward prolongations of the cupule of the nuchal skeleton.
- Fig. 17 b. Section through the medullary tube posterior to preceding, showing the endsac opening by the proboscis-pore into the medullary tube (see Text).
- Fig. 17 c. Similar section still farther back, showing the coecal (post-trematic) extensions of the end-sac.

This section passes near the termination of the anterior transverse lumen of the medullary tube, and a minute cavity, forming one of the system of separate medullary cavities into which the primitive lumen is subdivided, is seen in the dorsal wall of the tube.

Fig. 18. Portion of section through the collar-region, about half-way between the anterior neuropore and the buccal orifice of the stomochord. It passes through the middle of the nuchal portion of the stomochord, which is here fragmented into three divisions.

The section also passes shortly behind the end of the ventral coecum (coelomic canal) of the proboscis, and the alary processes of the nuchal skeleton have united behind the coelomic canal to form the keel. The small dorsal moiety of the skeleton is the body. Below the keel is a thick epithelial pad, projecting from the roof of the mouth (cf. Pl. XXVIII. Fig.  $1\,b$ ).

Fig. 19 a-b. Dorsal portions of sections through the collar.

Fig. 19 a shows the distal end of the first root entering the epidermis.

Fig. 19 b shows the proximal or basal portion of the first root close to the dorsal wall of the medullary cord shortly in front of its origin from the latter; and the intra-epidermal canal proceeding from the second root. The collar coelom is seen to be traversed by radial trabeculae enclosing radial muscles.

#### PLATE XXX.

Figs. 20-23 refer to Pt. carnosa.

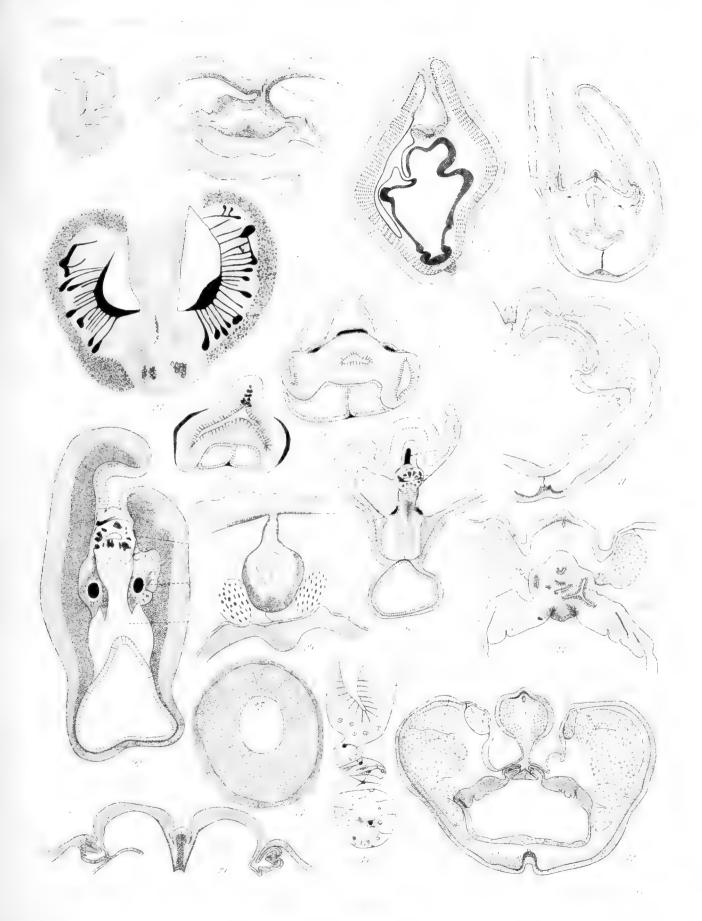
- Fig. 20. Section through collar-canal.
- Fig. 21. Dorsal portion of section through region of transition from collar to trunk, passing immediately in front of, and cutting tangentially the lip of, the posterior neuropore. To the left of the point of junction of medullary-tube and epidermis is seen the posterior end of the dorsal septum of collar. The collar canals are fused at one side with the wall of the first gill-pouch on each side, and with the basal angles of the medullary tube at their mesial sides. This association of collar-pores, first gill-pores and posterior neuropore constitutes the posterior trematic complex of Enteropneusta (see p. 320).
- Fig. 22. Section through anterior branchial region, showing the absence of gonads and the ventral coecum of the gill-pouch. On the left side the section passes through a tongue-bar and on the right through a septal bar; on the right of the figure the section is diagrammatically made to pass exactly between two successive gill-pouches so that nothing is seen of them. The thin layer of circular muscles which occurs outside the longitudinal muscles is not shown in the figure.
- Fig. 23. Section through the branchiogenital transition shortly behind the terminal gill-pores, showing the post-branchial canal (cf. Pl. XXVIII. Fig. 7).

#### Figs. 24-35 refer to Pt. ruficollis, n. sp.

- Fig. 24. Section through anterior end of central complex of proboscis in front of the stomochord, showing the bifurcation of pericardium with the radial vessels of the glomerulus. Between the two halves of the pericardium is seen the median septum of the proboscis, containing dorso-ventral muscles.
- Fig. 25. Section through the dilated region of the stomochord with its lateral pouches. Above the stomochord are seen the dorsal coelomic canals separated by the pericardium.

The coelomic epithelium overlying the efferent vessels of the proboscis is ciliated. Above the dorsal border of the pericardium are the two primary branches of the advehent dermal vessel of the proboscis. Between pericardium and stomochord is the central blood-space; and below the stomochord are the ventral coelomic canals separated by the ventral septum of the proboscis.

- Fig. 26. Section shortly posterior to preceding, showing the lateral pouches of the stomochord uniting across the middle line to form the ventral coecum of the stomochord which overhangs the ventral coelomic canals. On each side are seen the anterior rami of the cupule of the nuchal skeleton.
- Fig. 27. Section through the region of the proboscis pore, showing the efferent vessels lying in the scanty chondroid tissue and the alary processes of the nuchal skeleton arching over the united ventral coelomic canals (ventral coecum of proboscis).
- Fig. 28. Section through region of anterior neuropore, i.e. through the region of the insertion of proboscis into collar, showing the lobe-like ventral coecum of proboscis below the keel of the nuchal skeleton.





The dorsal vessel is cut approximately at the point whence it is continued forwards into the central blood-space, and where it gives off, dorsally, the advehent dermal vessel of the proboscis.

- Fig. 29. Dorsal portion of section through the collar, showing the medullary tube, somewhat flattened laterally, with central canal and solid root passing direct to the epidermis.
- Fig. 30. Dorsal epidermal portion of section through branchial region immediately behind collar, showing the posterior ends of the collar-pores. On the left the second gill-pore is cut tangentially and is seen to be overhung by the tongue-like fold of the collar canal. On the right of the figure the section passes between the first and second gill-pores, and shows the raphe in the middle of the tongue-like fold of the collar-canal (see Text).
- Fig. 31. Portion of section through branchial region, showing the gonad attached by a genital duct to the epidermis at the outer side of the branchial groove.
- Fig. 32. Section through the posterior end of the branchial region, showing the local depression of the branchial grooves and reduction of the branchial portion of the gut. The penultimate gill-pouches are seen at the bases of the grooves. At the outer and upper sides of the grooves are seen the anterior portions of the lateral septa (close to their anterior termination), enclosing the medial branches of the gonads.
- Fig. 33. Section shortly behind preceding, showing the anterior portion of the post-branchial canal with its subdivided lumen, and below it a pair of grooves continued back from the last pair of gill-slits.
- Fig. 34. Section through mature ovarian ovum, showing refringent inclusions in the nucleolus of the germinal vesicle. Highly magnified.
- Fig. 35. Ventral portion of section through hind-gut, showing the pygochord with its vacuolated cells.

#### PLATE XXXI.

#### Figs. 36-45 refer to Spengelia porosa.

- Fig. 36. Central portion of section through proboscis in front of the central complex, showing the vermiform process lying in the median septum, through which pass the dorso-ventral muscles. On each side of the median septum is the central cavity of the proboscis, the dorsal side of which is bounded by decussating conjunctive fibres.
- Fig. 37. Section through the commencement of the central complex, showing the anterior projecting horns of the glomerulus, between which lies the vermiform process of stomochord.
- Fig. 38. Section through the posterior end of the dilated region of the stomochord, shortly behind the glomerulus, showing the basal organs of the proboscis enveloped in chondroid tissue. The epidermis is omitted. The lower division of the stomochord is the ventral coecal dilatation, which projects backwards into the cupule of the nuchal skeleton and so appears in section at this level separate from the smaller dorsal division. On either side of the dorsal division of the stomochord are seen the dorsal coelomic canals (p), of which the left is the larger in this region (on the right of the figure), and communicates at a slightly anterior level with the end-sac, which is seen above the pericardium. The ventral coelomic canals are nearing their termination in the chondroid tissue.

Fig. 39. Section passing through the proboscis-pore (external opening of end-sac). It may be noted how the substance of the nuchal skeleton grades off into the chondroid tissue. Above the stomochord the dorsal vessel is seen to give off the advehent dermal vessel of the proboscis, on either side of which are the anterior extremities of the perihaemal cavities.

Fig. 40 a-c. Sections through the vestigial root of Sp. porosa.

Fig. 40 a shows the distal terminal vesicle with its thick wall enclosing mucoid contents. Zeiss Oc. 3, Obj. D.

Fig. 40 b (posterior to preceding and less highly magnified) shows the root itself abutting upon and terminating in the distal vesicle, the wall of which is cut tangentially, and encloses a homogeneous mass of darkly staining matter.

Fig. 40 c (still farther back) shows the basal portion of the root and its origin from the dorsal wall of the medullary cord.

Fig. 41. Section through the middle of the collar nerve-cord (medullary cord), showing medullary cavities and distribution of fibrous layer.

Fig. 42. Section through collar-canal.

Fig. 43. Cross-section of the skeletal rod of a septal bar with blood-vessel at inner end; taken from a horizontal section through the pharynx.

Fig. 44. Section through posterior end of collar with posterior neuropore, showing the truncal canals in the perihaemal cavities. On the left the figure shows the truncal canal opening into the first gill-pouch at the level of the collar-funnel; on the right the truncal canal is seen at a more anterior level, and the posterior end of the peripharyngeal cavity of that side is seen lying against the wall of the throat (collar-gut), while imbedded within the wall is the posterior extremity of one of the cornua of the nuchal skeleton.

Fig. 45. Section through the branchial region, showing medial gonads, inner circular muscles and oesophageal portion of gut. On the right is shown a tongue-bar and on the left a septal bar with the cut ends of the synapticula.

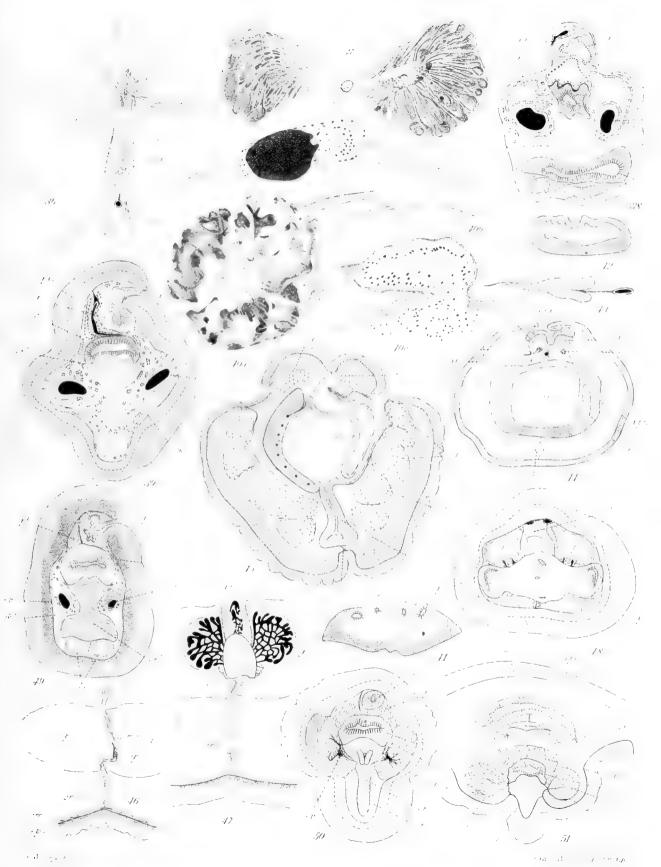
#### Figs. 46-51 refer to Sp. alba, n. sp.

Fig. 46. Portion of section through proboscis in front of central complex (cf. Fig. 36).

Fig. 47. Portion of section through commencement of central complex. The section passes immediately in front of the anterior end of the pericardium, and shows the two anterior horns of the glomerulus on either side of the stomochord. Above the latter is seen the vascular complex which constitutes the dorsal recurrent dermal vessel of the proboscis.

Fig. 48. Section through base of proboscis passing through the pouched region of stomochord, shortly behind the glomerulus, the continuation of which into the efferent vessels is seen below the ventral epithelium of the dorsal coelomic canals (cf. Pl. XXX. Fig. 25). The pericardium is seen to be traversed by transverse fibres, and above it are the two primary branches of the advehent dermal vessel. The dorsal and ventral coelomic canals are separated by the lateral pouches of the stomochord.

Fig. 49. Section through the neck of the proboscis in the region of the proboscis-pore, passing in front of the posterior termination of the ventral coelomic canals. The chondroid substance is homogeneous, and is characterised by the relative scarcity of cellular islets.



WILLEY ENTEROPNEUS '\*

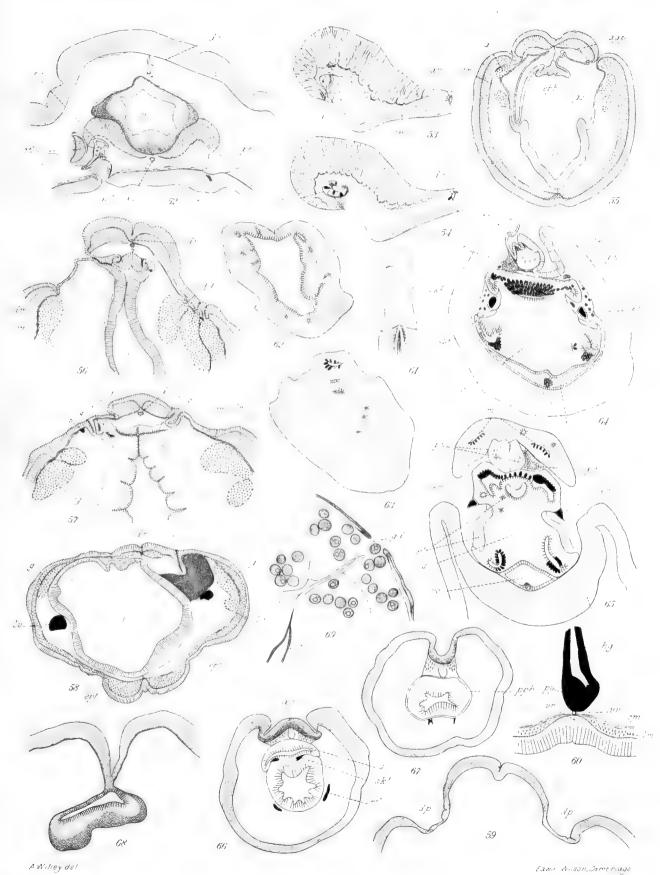
- Fig. 50. Similar section at a more posterior level (behind the ventral coelomic canals), showing the post-trematic coecal projection of the end-sac into the anterior end of the left perihaemal cavity. This section with the next shows the inclusion of the fused anterior portions of the cornua of the nuchal skeleton within its body, which presumably takes place concomitantly with the progressive growth in length of the animal.
- Fig. 51. Portion of section shortly behind the insertion of proboscis into collar, showing the medullary tube (which opens at a slightly more anterior level, independently, by the anterior neuropore) and the anterior epidermal involution (anterior Epidermistasche), formed by backward extension of the angle of insertion of proboscis and collar, dorsal to the medullary tube with which it is united by a short septum.

#### PLATE XXXII.

Figs. 52-60 refer to Sp. alba.

- Fig. 52. Portion of section through region of transition from collar to trunk, but in front of the posterior neuropore. On the left of the figure the truncal canal is seen communicating with the first gill-pouch at the commencement of the first gill-slit and at the level of the collar-funnel. On the right of the figure the section passes in front of the truncal canal of that side.
- Fig. 53. Section through one of the perihaemal cavities immediately in front of a truncal canal. At x is seen a distinct loculus for the reception of the truncal canal; this loculus extends over several sections.
- Fig. 54. Section through the same perihaemal cavity at a level intervening between Fig. 52 and Fig. 53, showing the truncal canal as an independent tube.
- Fig. 55. Section through branchial region. On the left a tongue-bar is shown, and on the right the figure shows the entire half of a gill-slit between septal bar and tongue-bar. Note absence of medial gonads, presence of inner circular muscles and of a minute dorsal diverticulum of the gill-pouch (dgp).
- Fig. 56. Upper half of section through the branchiogenital transition, showing accessory gonads and last gill-slit.
- Fig. 57. Similar section through posterior end of genital region (genito-hepatic transition), showing intestinal canals and pores (vestigial gill-slits). Owing to the overlapping of these canals, as described in the text, portions of no less than five of them are seen to the left of the figure and two on the right. They consist of ectodermal and endodermal portions, and occur at the dorsal angles of the gut, in the same position as the terminal true gill-slits (cf. preceding figure).
- Fig. 58. Section through the hepatic region, showing the gonads continued into this region, the internal hepatic saccules (that on the right cut tangentially), an intersaccular epidermal involution, the lateral longitudinal vessels and the ventro-lateral epidermal tracts.
- Fig. 59. Portion of section through epidermis of genital region, to show the depth of the dermal pits in this species and individual.
- Fig. 60. Ventral portion of section through caudal region, to show the thickened median ventral wall of hind-gut representing the pygochord.

- Fig. 61. Pt. biminiensis, n. sp. Dorsal view of anterior end, showing convergence and overlapping of genital pleurae at anterior end of trunk.
- Fig. 62. Same. Section through body of stomochord in front of the pouched region, showing wide cavity.
- Fig. 63. Same. Section through anterior portion of the coecal region of stomochord in front of the pouches.
- Fig. 64. Same. Section through neck of proboscis in region of proboscis pores (see Text). Between the right and left end-sacs is seen the anterior extremity of the right perihaemal cavity, and below the right end-sac (left of figure) the solid posterior extremity of pericardium. Note dorso-lateral and ventro-lateral pouches of stomochord (cf. Pl. XXIX. Fig. 17 a). Above the latter are seen the anterior rami of the cupule of nuchal skeleton.
- Fig. 65. Same. Portion of section behind region of insertion of proboscis into collar, showing the post-trematic extension of the left end-sac, the anterior paired lumen of the medullary cord with two separate medullary cavities, the process of skeletal substance enclosed within the stomochord between the dorso-lateral pouches; and the confluent ventral coelomic canals (ventral coecum of proboscis cavity).
- Fig. 66. Pt. flava. Section through anterior collar-region of regenerating specimen shown in Pl. XXVI. Fig. 5 A, to show formation of medullary tube by medullary folds. The section cuts the anterior border of buccal orifice of stomochord tangentially.
- Fig. 67. Same. Similar section through middle of collar-region of same specimen as preceding, showing appearance of medullary groove at this level.
- Fig. 68. Same. Portion of section through extreme anterior end of collar region of regenerating individual shown in Pl. XXVI. Fig. 5 B, to show the fusion of the medullary folds over the medullary tube at this level. Posterior to this point the medullary canal is still unclosed in this specimen.
- Fig. 69. Pt. ruficollis. Dorso-lateral portion of section through genital region of mature female, to show the wide gaping of the genital duct.



WILLEY. ENTEROPNEUSTA.

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ON A COLLECTION OF ECHIURIDS FROM THE LOYALTY ISLANDS,
NEW BRITAIN AND CHINA STRAITS, WITH AN ATTEMPT TO
REVISE THE GROUP AND TO DETERMINE ITS GEOGRAPHICAL
RANGE.

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WITH PLATE XXXIII.

#### PART I.

#### ON THE COLLECTION.

The collection of Echiurids brought back from the Eastern Seas by Dr Willey was small. It yielded but one species of Bonellia, the widely distributed *B. viridis*, and four species of Thalassema. With the exception of *Th. kokotoniense* described by Fischer, from the East Coast of Africa, all these had been before taken from neighbouring localities.

In Part I. of the following article references to literature have been omitted, but these are fully given in Part II.

## I. GENUS. BONELLIA, Rolando.

#### 1. Bonellia viridis, Rolando.

One small specimen, measuring 1.5 cm. in the body and 2 cm. in the proboscis, of which the forked portions formed about 1 cm.

The hooks protruded very far.

W. III.

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The single nephridium was on the right side and was full of ova; other eggs in an equally advanced state lay in the coelom.

The eggs contained large oil globules, 6 or 8 arranged more or less in a ring round the circumference, giving the more opaque protoplasm somewhat the appearance of a star.

Neither in the nephridium nor in the oesophagus did I succeed in finding any males. Locality. Lifu, Loyalty Islands.

## II. GENUS. THALASSEMA (Gaertner), Lamarck.

## 2. Thalassema baronii, Greef.

Four specimens from Sandal Bay, Lifu, Loyalty Islands, and one from China Straits, British New Guinea. They were in a very contracted condition, and almost as broad as long. The largest measured, with the proboscis, rather over 3 cm. in length, the smallest had an inclusive length of 2 cm. (Figs. 1 and 7, Plate XXXIII.) The number of longitudinal muscle-bands is 17 or 181 in the largest specimen which I opened. Of the four nephridia, three were much distended and full of eggs, the left anterior nephridium contained no ova and was of small size. The ova are spherical. In his Monograph, Greef states, "Weibchen...bisher nicht beobachtet," so that it is interesting to confirm his surmise that the female resembles the male in colour, size and organisation.

Dr Willey characterises this species when alive as "compact, opaque and warty."

#### 3. Thalassema diaphanes, Sluiter.

One specimen. The body and the proboscis are both strongly curved, so that the whole animal resembled the figure 3. The length of the body is about 3 cm.; when straightened, its diameter, which is very uniform, is about 7 mm., and the length of the proboscis is a little over 2.5 cm. (Fig. 2, Plate XXXIII.)

The papillae, not all of one size, are closely aggregated round the anterior end of the body, they become more sparse towards the middle, and, except on the inner edge of the curved body, they almost disappear on the posterior half, with the exception of the extreme posterior end, where they are large.

The skin in the spirit specimen is of a dirty brown colour and fairly transparent, except where the papillae are most closely set.

I have no doubt that this specimen is of the same species as Sluiter's Th. diaphanes. Its proboscis, however, is not truncated, but roundly pointed, and the alimentary canal was filled with irregular blocks of coral rock, not with pellets of mud.

<sup>&</sup>lt;sup>1</sup> Fischer (Abh. Ver. Hamburg. Vol. XIII. 1895, p. 1) has re-investigated Greef's original specimen of the Th. baronii and has determined the number of longitudinal bands of muscle to be 18—19, the same number that Greef indicates in his figure. Lampert by some inadvertence gives the number at 23, and this number is copied by Rietsch.

Whether the contents of the intestine is filled with pellets regularly arranged or not seems to me a matter of diet and of no systematic importance.

LOCALITY. Pigeon Isle, New Britain.

#### 4. Thalassema erythrogrammon, Max Müller.

One specimen, from China Straits, British New Guinea. The representation on Plate XXXIII. Fig. 4, is taken from a sketch made by Dr Willey on the spot from the living animal. It is about natural size. He further made notes as to the colouring, from which it appears that the animal is pigmented in a very lively and gay manner, and with the Italian national colours. The proboscis is in the living state white, but this passes gradually into green at the edges. The body is longitudinally striped in alternate strips of red and white, and during the contractions rings of "rounded, red, node-like prominences" are produced, probably papillae. An attempt to reproduce their appearance is made in Figure 4, but they are not confined to the narrow band there indicated. The tail is white and papillated.

During life incessant peristaltic contractions passed from before backwards, and during each constriction the above-mentioned red spots come into prominence.

LOCALITY. The single specimen was taken from sand under stones on the exposed reef at Matadona.

#### 5. Th. kokotoniense, Fischer.

A single specimen. The colour, in the spirit specimen, was ivory white, the longitudinal muscles were clearly visible through the skin; at the posterior end the skin was wrinkled in circular folds, and the arrangement of the papillae produces a slight circular striation. Fig. 3, Plate XXXIII.

The length of the trunk was, in the spirit specimen, 4.5 cm., its greatest breadth 1.7 cm., the length of the proboscis 1.2 cm. The latter is deeply grooved, and its edges approximated in the contracted state.

The number of longitudinal muscles was 18. The three pairs of nephridia increase uniformly in size from before backward, the anterior or smallest pair opening in front of the setae.

The food in the alimentary canal was soft brown mud, arranged in definite pellets. I did not find that the anal trees were longer than the body, as was the case with Fischer's specimen, but doubtless their state of contraction and expansion varies.

LOCALITY. Blanche Bay, New Britain.

#### PART II.

## AN ATTEMPT TO REVISE THE GROUP ECHIUROIDEA.

In determining the species of the Echiurids collected by Dr Willey during his voyage to the East in 1895—97, a considerable difficulty arose owing to the scattered nature of the literature referring to the more recently described species. The number of these species has very much increased since the publication of Greef's Monograph in 1879, and has even doubled since the date of Rietsch's Thesis, 1886, so that little excuse is needed for an attempt to revise the group. In the following pages I have taken Greef's Monograph as a starting point, and must refer to his work for the literature prior to the date of his publication—except for one or two papers there omitted—for the list of synonyms, and for an account of a small number of species which for the most part are too inadequately described to be satisfactorily recognisable.

#### THE DETERMINATION OF THE SPECIES.

In determining the species of an Echiurid, the following facts are of importance:-

- (I.) The size both of the trunk and of the proboscis. Echiurids are extremely extensile, and so the limits of their size vary widely. When killed, as a rule the animal contracts violently, but this is by no means always the case, and I have given on Plate XXXIII. Figs. 5 and 6, the outlines of two specimens of *Th. neptuni*, both supplied by the Plymouth Laboratory, and both of about the same weight, but one has been killed expanded and the other contracted; it will be seen that the difference in outline is remarkable.
- (II.) The colour. This is only of value when described from the living animal, in which, however, it seems to vary a good deal both in different individuals and in the same individual in different states of contraction. Echiurids are often very brilliantly coloured, the bright green Bonellias and Thalassemas and the deep red Thallasemas, with their violet stripes and white spots, form very striking objects until they are put in spirit, when the colour rapidly fades. It is interesting to notice that many of these creatures pass their lives hidden in holes in rocks, or sunk in mud or sand, where their gorgeous colour is concealed, and, as far as we can see, is of no use to the animal.
- (III.) The papillae. These are, as a rule, wart-like elevations, scattered more or less uniformly over the surface of the body. In a few cases they show a tendency to arrange themselves in rows, but this is rare, and their specific importance is on the whole small.

<sup>&</sup>lt;sup>1</sup> Published also in the Recueil Zool. Suisse, Vol. m. p. 313.

- (IV.) The posterior ring or rings of bristles found in the genus *Echiurus* is of great systematic value, but in counting the bristles it must not be forgotten on the one hand that they often fall out, and on the other it seems probable that the replacing bristle is sometimes counted as well as the one it is to replace.
- (V.) The longitudinal muscles. These are especially valuable in the genus *Thalassema*, and serve to readily divide it into two groups, those with a continuous sheath of longitudinal muscles, and those with the sheath broken up into bundles. Some species have been practically founded on the number of such bundles. As a rule the number is small, *i.e.* below twenty. In using this as a criterion of species it must not be forgotten that the muscles sometimes fuse and anastomose, thus diminishing or increasing the number at any one level. I think it probable, but have no proof, that they also increase in number with advancing age.
- (VI.) The number of nephridia. These vary from a single one on the right side or on the left, up to three pairs. They are perhaps the most valuable aids to specific identification that the animals present.
- (VII.) The anal trees. The variations in size presented by these organs are due for the most part to the state of contraction or expansion in which they were found at the moment of death and are of little specific importance. Of greater value is the primary or secondary branching of the diverticula which bear the funnels.

In the following account I have arranged the structures of each species under the above headings and in the above order, adding here and there any other details which seem to help in identifying the species in question. As far as may be I have given the colour of the living animal, but the colour of the animal, live or dead, is sometimes omitted in the original descriptions, and more often it is not mentioned whether the colour is natural or the result of reagents. For myself whenever I see "yellowish-brown," "greyish-yellow," and such sober hues, I suspect spirit.

Until the ideal arrangement of concentrating all the type specimens of a group into one Museum is attained, it is impossible to form a very definite opinion as to the value of many species, and therefore in the following list I have practically included all the species whose descriptions I could find. I am not however prepared to think that they will all stand the test of time, and I am most doubtful about those whose claim to specific rank rests on one more or one less in the number of the longitudinal muscle bundles, and about those described from single, sometimes fragmentary, specimens.

The only description of a *Thalassema* which I have not incorporated in the following lists is that of *Th. verrucosa* Studer<sup>1</sup>, from Betsy Cove, Kerguelen. It is too meagre to permit of an opinion as to whether the species is new, or to fit into the key to the species. The number of species of *Bonellia* and *Echiurus* is small, and they do not require a key, but I have endeavoured to supply such an aid to identification in the

case of the genus *Thalassema* where the number of species is some twenty. The key is based on one suggested by Lampert, and in the main depends on the number of nephridia and on the number of bundles of longitudinal muscles, where such exist.

I agree with Lankester that there does not seem sufficient reason to separate Horst's *Hamingia glacialis* from the *Hamingia arctica* of Koren and Daniellsen, so that this genus is left with but one species, whilst as to *Saccosoma* but one specimen has ever been seen.

The various species are arranged in the following list, alphabetically. The contractions in the references to literature are those suggested by Mr D. Sharp, the Editor of the Zoological Record.

## GENUS I. BONELLIA. Rolando<sup>1</sup>.

Luigi Rolando, Professor of Anatomy in the Royal University of Turin, dedicated this genus to his colleague, Andrea Bonelli, who was Professor of Zoology at the same University and Sub-Director of the Museum of Natural History.

Species 1. Bonellia minor. Marion.

Rietsch. Études sur les Gephyriens armés ou Échiuriens. Thesis. Geneva, 1886, and Recueil Zool. Suisse, Vol. III. p. 313.

Length of body 1.5 to 3 cm. Length of proboscis when extended some 20 cm.

Colour, dark green.

Longitudinal muscles continuous.

Nephridium, single, usually to the left.

Anal trees ramify but once before ending in funnels.

Male with recurved and pointed hooks, not ciliated on the back, which is transversely marked or ringed. Larva with a ventral sucker.

LOCALITY. Bay of Naples and Marseilles.

Species 2. Bonellia pumicea, Sluiter.

Sluiter. Natuurk. Tydschr. Nederl. Ind. Vol. L. Ser. 8, Vol XI. 1891, p. 111.

Described from a single specimen.

Length of body of female 5 mm. Length of proboscis about the same, but can be stretched to 1 cm.

Colour, light green with a reddish shimmer, the proboscis is milk white.

Papillae are in the form of light white spots, and are mostly aggregated at the two poles of the body.

<sup>1</sup> Mem. Ac. Turin. Vol. xxvi. 1821, p. 539.

Nephridium, single.

Anal trees, more tube-like than sac-like, the diverticula branch twice or thrice before ending in funnels.

Males found in oesophagus only. They have a pair of hooks, and further differ from those of *B. viridis* in having the opening of the vas deferens not terminal but posterior to the hooks on the ventral surface, and in having the posterior half of the body drawn out into a narrow tail.

LOCALITY. The female was found in a piece of pumice-stone dredged from a depth of 9 faths., not far from Krakatoa.

Species 3. Bonellia suhmii. Selenka.

Selenka. Challenger Reports, Vol. XIII. Pt. XXXVI. 1885, p. 9.

Selenka had only a single specimen, which was first described—not altogether correctly—by Willemoes-Suhm. The specimen wanted both proboscis and posterior end of body. Selenka's description is very meagre, but he does not doubt that it is a new species.

Length of body, without hinder end, 8 cm.; greatest breadth 2.9 cm.

The body tapers posteriorly and on the whole it is somewhat club-shaped.

Colour, not stated.

Papillae. Certain wart-like structures covered the skin anteriorly and posteriorly, leaving a broad smooth band where the diameter of the body is greatest.

Longitudinal muscles, not mentioned.

Nephridium, single, and from the sketch I take this to be on the right side.

Anal trees, the primary branches bear the funnels.

No male was found either in oesophagus or in the single nephridium which contained eggs.

Locality. Lat. 41° 14′ N. Long. 65° 45′ W. off Nova Scotia. Depth 1340 faths. Dredged from blue mud.

SPECIES 4. Bonellia viridis. Rolando.

Greef. Acta Ac. German. Vol. XLI. Pt. II., 1879, p. 154.

Haswell. P. Linn. Soc. N. S. Wales, Vol. x. Ser. I., 1886, p. 331,

Marcialis. Boll. Soc. Rom. Zool. No. 1, p. 246.

Kükenthal and Weissenborn. Jena Zeitschr. Vol. xix. 1886, p. 776.

Norman. Ann. Nat. Hist. Ser. vi. Vol. XIII., 1894, p. 150.

Koren and Danielssen, Fauna Littoralis Norwegiae. 3rd Hft., 1877, p. 151.

After carefully reading Rolando's description of *Bonellia fuliginosa*, I am inclined to the opinion of Greef that the animal he describes is not specifically distinct from *Bonellia viridis*.

Length of body some 15 cm.; of proboscis, when fully extended, 150 cms.

Colour, dark green, almost black green, the ventral middle line is lighter.

Papillae appear as dark, scattered spots, all over the body.

Longitudinal muscles continuous.

Nephridium single, usually that of the right side.

Anal trees, short and sac-like with diverticula which branch twice before ending in funnels.

Sexes unlike. Male small and parasitic in female, with no hooks, uniformly ciliated and not annulated. Larva with no ventral sucker.

LOCALITY. Mediterranean, Adriatic; Port Jackson, Australia; at Dyveholmen on the West coast of Norway; Trondhjem Fjord, Bergens Fjord, and Kors Fjord. In the last-named two places the animal was dredged at a depth of 50—100 faths., on a sandy bottom. Besides the Loyalty Islands where Dr Willey's specimen was taken, this species was seen by him in the D'Entrecasteaux Group, British New Guinea.

#### GENUS II. ECHIURUS. Guérin-Méneville1.

The generic name *Echiurus* seems to have been first used by Guérin-Méneville for Pallas' genus *Lumbricus echiurus*. Cuvier had previously used the word "echiures" but not in a generic sense. Guérin-Méneville attempts no description of the genus, but he names it and gives a satisfactory figure of *Echiurus pallasii*. The date on the titlepage is 1829—1843, but Mr Davies Sherborn has been kind enough to tell me that the plate dealing with *Echiurus* was not published by January 1831, although the name was in full use in 1835<sup>2</sup>. Guérin-Méneville's text was published as a whole in September 1844.

Species 5. Echiurus chilensis. Max Müller.

Greef. Acta Ac. German. Vol. XLI. Part II., 1879, p. 144.

Fischer. Gephyreen Hamburger Magalhaensische Sammelreise, 1896.

Synonym. E. farcimen, Baird. J. Linn. Soc. Vol. XI. 1873, p. 97.

Baird's specimens differ in no important detail from *E. chilensis*, but are rather bigger, the largest attaining a length of 16 ins.

Length of body variously given as 6.5 ins., 14 cm., 16 ins. Diameter of body 3 cm. Length of proboscis 6—7 mm.

Colour, faint yellowish grey.

Papillae almost uniformly distributed over the body, and except at the hinder end, very close together. A single ring of 11 bristles.

<sup>1</sup> Iconographie du rèone anim. de Cuvier, Zoophytes, p. 9, and Plate VI, fig. 3.

<sup>&</sup>lt;sup>2</sup> J. F. Brandt, Prodromus Animalium ab H. Mertensio, in orbis terrarum circumnavigatione observatorum. Petrop. 1835. 4to. Wiegmann's Archiv, 1836, 11. p. 188.

Nephridia, three pairs.

Anal trees, 1.75" long, or 3 cm. long, light brown. Fischer was not able to find any ciliated openings on them.

LOCALITY. Punta Arenas, Straits of Magellan.

Species 6. Echiurus forcipatus. Reinhardt.

Greef. Acta Ac. German. Vol. XLI. Pt. II., 1879, p. 143. Koren and Danielssen, Fauna Littoralis Norwegiae. 3rd Hft. 1877, p. 151.

Synonym. Echiurus lütkeni. Diesing.

Size of body, larger than the average of *E. Pallasii*. Hansen's specimens from the Sønd Fjord measure 4.6 cm. in body-length, 2 cm. in diameter, and 1.4 cm. in the proboscis.

Colour, greyish-green.

Papillae not in very definite rings, forming anteriorly and posteriorly irregular "plaques." Two rings of bristles, the anterior with 9—10, the posterior with 7 bristles, in Hansen's specimens the number of bristles were 7 anteriorly and 6 posteriorly.

LOCALITY. Coast of Greenland, and the Sønd Fjord. The details of this species are very inadequate and I can only re-echo Greef's remark. "Echiurus forcipatus bedarf somit, meiner Meinung nach, rücksichlich seiner Artselbstständigkeit einer weiteren Prüfung."

Species 7. Echiurus pallasii. Guérin-Méneville.

Greef. Acta Ac. German. Vol. XLI. Pt. II., 1879, p. 136. Koren and Danielssen, Fauna Littoralis Norwegiae, 3rd Hft. 1877, p. 151.

Length of body, 10—15 cm., including proboscis. Diameter of body, 3—4 cm. Length of proboscis, 3—4 cm.

Colour, grey or greyish yellow to a deep yellow or orange.

Papillae arranged in more or less definite rings, of which there are 20—23 rings of large papillae, and between each of these 3—5 rings of smaller papillae. Two rings of bristles, the anterior with 8, the posterior with 7 bristles.

Nephridia, two pairs.

Anal trees, long, simple, brown tubes.

LOCALITY. North Sea, English Channel, the Sound, North Atlantic, in the Christiania Fjord and the øx Fjord (Finmark). It lives in soft sand, mud or clay. Apparently this animal was formerly used by the fishermen of the Belgian and German coasts as bait, though it is doubtful if it is now so used.

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Species 8. Echiurus unicinctus. Von Drasche.

Von Drasche. Verh. Ges. Wien. Vol. XXX. 1881, p. 621. Selenka. Challenger Reports. Vol. XIII. Pt. XXXVI. 1885, p. 6. Fischer. Abh. Ver. Hamburg. Vol. XIII. 1895, p. 21.

Length of body averages 8.5 cm., length of proboscis, 5—6 mm. when contracted. Colour, bright yellowish brown.

Papillae uniform in size, only arranged in transverse rows in special places, e.g. near the hooks. Single circlet of bristles, usually 11, but any number from 9—13 has been found.

Circular muscles consist of some 200 bundles frequently anastomosing. Nephridia, two pairs, with spirally coiled internal openings.

LOCALITY. Inland Sea, Japan, "Amurlande"? Amur Bay. This species is found in the mud near the shore. It is used by the Japanese fishermen as bait.

## GENUS III. HAMINGIA. Koren and Danielssen.

The authors of this genus named it after Hamingja, "the Fortuna of Northern Mythology."

Species 9. Hamingia arctica. Koren and Danielssen.

Koren and Danielssen. Norwegian North Atlantic Expedition: Zoology, Gephyrea, 1881, p. 20.

Horst. Nederl. Archiv Zool., Supplementalband, I. 1881.

Lankester. Ann. Nat. Hist. Ser. v. Vol XI, 1883, p. 37.

Synonym. Hamingia glacialis, Horst.

Length of body of female, 12 cm., diameter, 2 cm., length of proboscis, 1.5 ins. or "as long as the body" in Lankester's specimen. The proboscis is not forked.

The genital setae are absent in the female.

Colour, light or dark grassy green.

Longitudinal muscles, continuous.

Nephridia, single or one pair, each opens on a well-marked papilla.

Anal trees, branched, twice or thrice before ending in funnels; brown.

The males resemble those of *Bonellia viridis*, but have hooks like those of *B. pumicea* and *B. minor*, but the vas deferens opens in front of the hooks in *Hamingia*. They occur in the dilated pharynx of the female.

LOCALITY. Two hundred miles north of the North Cape, and in the Hardanger Fjord, Lat. 60° at a depth of 40 fathoms.

GENUS IV. SACCOSOMA. Koren and Danielssen.

From " $\sigma \alpha \kappa \kappa \sigma s = \operatorname{sack}$ ,  $\sigma \hat{\omega} \mu a = \operatorname{body}$ ."

Species 10. Saccosoma vitreum. Koren and Danielssen.

Koren and Danielssen. The Norwegian North Atlantic Expedition: Zoology, Gephyrea, Christiania, 1881, p. 34.

Described from a single specimen.

Length of body, 3 cm., 5 mm. broad. Proboscis absent.

Colour, white shot with red anteriorly and posteriorly, the middle of the body is colourless.

Skin anteriorly and posteriorly thick and rugose, but thin and transparent round the centre of the body.

Longitudinal muscles in numerous bundles—but the number is not stated—in the anterior part of the body; they fuse into a continuous sheath, about half-way down the animal.

Nephridium, single, that of the left side.

The material inside the intestine is arranged in pellets.

Anal trees, not found.

Locality. Dredged at a depth of 1215 fathoms, about half-way between Iceland and Norway, from a bottom of "sabulous clay."

#### GENUS V. THALASSEMA (Gaertner). Lamarck.

Pallas in his "Spicilegia" mentions the name *Thalassema* as used by Jos. Gaertner. but he himself calls the animal in question *Lumbricus thalassema*. It would seem that Lamarck in his *Système des Animaux sans Vertèbres*, 1801, p. 328, was the first to use the word *Thalassema* generically. His statement that the word is used in Cuvier appears to be erroneous. It is in full use in the edition of Buffon, Vers. I. 1802, p. 225.

I am indebted for the above particulars to the kindness of Mr Davies Sherborn.

Species 11. Thalassema baronii. Greef. Plate XXXIII. Figs. 1 and 7.

Greef. Acta Ac. German, Vol. XLI. Pt. II. 1879, p. 151.

Shipley. "Notes on a Collection of Gephyrean Worms formed at Christmas Island by C. W. Andrews," P. Zool. Soc. London, 1899.

Length of body, 7—8 cm. Length of proboscis, 5—6 cm.

Colour, dark green, with violet longitudinal stripes, and with white specks—papillae—irregularly scattered all over the body. The dorsal side of the proboscis is light green, the ventral is of a brownish flesh colour.

Longitudinal muscles, 17—19 bundles.

Nephridia, two pairs, with spirally coiled internal openings.

Anal trees, long, brown, pointed anteriorly. They bear short branching outgrowths.

LOCALITY. Lanzarote, Canary Islands, among lava blocks and stones. Bahia 7—20 faths. Christmas Island, Indian Ocean, and at Lifu, Loyalty Islands.

## Species 12. Thalassema caudex. Lampert.

Lampert. Zeitschr. wiss. Zool. Vol. XXXIX. 1883, p. 340.

Shipley. P. Zool. Soc. London, 1898, p. 472.

Length of body very various from 5-7 cm. Length of proboscis, 1.8-2.5 cm. in the preserved specimens.

Colour, leather-brown or olive-green in spirit specimens. In the fresh state the animal is green with red longitudinal stripes and white spots or papillae.

Papillae, on the raised longitudinal ridges which correspond with the longitudinal muscles. They are very numerous and arranged in plaques posteriorly. Skin tough.

Longitudinal muscles, 16-18 bundles.

Nephridia, three pairs, with spirally twisted internal opening. The anterior pair open in front of the ventral hooks1.

Anal trees, two long brown tubes.

LOCALITY. Red Sea, Indian Ocean, Rotuma. At the latter place the specimens were found under growing coral near the edge of the Reef.

#### Species 13. Thalassema diaphanes. Sluiter. Plate XXXIII. Fig. 2.

Sluiter. Natuurk. Tijdschr. Nederl. Ind. Vol. XLVIII. 1888, p. 244.

Length of body, 3 cm. Length of proboscis, 3 cm. The proboscis forms a tube just before it joins the body and, in Sluiter's specimens but not in mine, the tip of the proboscis is broad and sharply truncated.

The skin is very thin and transparent. The papillae are little white specks scattered over the body, but rather more concentrated at the two poles.

Longitudinal muscles, continuous.

Nephridia, one pair, without spiral internal openings.

Anal trees, small, only 5 mm. long, transparent as glass.

The contents of the alimentary canal are aggregated in pellets, like those I found in Th. kokotoniense.

LOCALITY. Taken from the mud bottom of the Bay of Batavia at a depth of 10—12 fathoms. The animals live well in aquaria, hiding their bodies in the mud and stretching out their proboscis into the water. Also from Pigeon Isle, New Britain.

<sup>&</sup>lt;sup>1</sup> Lampert states this; I thought that in my specimens the anterior nephridia opened at the level or just behind the level of the ventral hooks.

Species 14. Thalassema erythrogrammon. Max Müller. Plate XXXIII. Fig. 4.

Greef. Acta Ac. German. Vol. XLI. Pt. II. 1879, p. 147. Von Drasche. Verh. Ges. Wien, Vol. XXX. 1881, p. 624. Sluiter. Natuurk. Tijdschr. Nederl. Ind. Vol. XLIII. 1884, p. 58.

Length of body, 8—16 cm. Length of proboscis about one-third to three-quarters of body-length.

Colour of proboscis, on the outer dorsal surface bright green, on the ventral, yellow, with a violet line on each side. The hinder end of body is violet, and longitudinally grooved, the grooves being light or dark red, according to the state of contraction. The Bourbon specimens in life were described as green, with red longitudinal stripes and white proboscis. The colour of Dr Willey's specimen is described in Part I. of this article.

Longitudinal muscles, arranged in 14 bundles.

Nephridia, three pairs, with spirally coiled internal openings.

Anal trees, very thin, brown.

A rectal diverticulum is present.

LOCALITY. Red Sea; Isle of Bourbon; Billiton, Malay Peninsula; China Straits, New Guinea. Amongst coral.

Species 15. Thalassema exilii. Fr. Müller.

Lampert. Zeitschr. wiss. Zool. Vol. XXXIX. 1883, p. 341.

The details of this species are furnished by Lampert from four specimens in the Berlin Collection, labelled "Thalassema exilii, Fritz Müller, Brasilien, Desterro, Fritz Müller." The description of the author of the species, if one existed, appears to be lost.

Length, 2.6 cm. The body expands posteriorly.

Colour, brown in spirit specimens.

Papillae, scattered irregularly from the middle to the posterior end of the body, but they are most strongly aggregated round the middle.

Longitudinal muscles, 8-10 bundles.

Nephridia, two pairs. The internal openings are folded and crinkled, not spirally twisted.

Anal trees, small.

Locality. Desterro, in Brazil.

Species 16. Thalassema faex. Selenka.

Selenka. Challenger Reports, Vol. XIII. Pt. XXXVI. 1885, p. 7.

Length of body, 4 cm. when contracted. Diameter, 1.5 cm.

Colour, whitish and the skin is smooth.

Papillae, indistinct and scattered.

Longitudinal muscles, undivided.

Nephridia, one pair.

Anal trees, moderate in size, bearing irregular branches, some simple, others much branched.

LOCALITY. Lat. 60° 34′ N., Long. 4° 40′ E. Off the coast of Norway. H.M.S. Porcupine.

Species 17. Thalassema formosulum. Lampert.

Lampert. Zeitschr. wiss. Zool. Vol. XXXIX. 1883, p. 339.

Length of body averages 3 cm. Length of proboscis, 8 mm. Diameter, 1 cm. Colour, white in spirit specimens.

Papillae white, scattered uniformly all over body, and nowhere arranged in rows. Skin very thin.

Longitudinal muscles, 7 or 8 bundles.

Nephridia, two pairs, with spirally twisted internal openings. Both pairs open behind the ventral hooks.

Anal trees, broad, sac-like organs.

A spherical diverticulum on the rectum.

LOCALITY. Cavite, near Manila; Shanghai.

Species 18. Thalassema gigas. Max Müller.

Greef. Acta Ac. German. Vol. XLI. Pt. II. 1879, p. 149.

Length of body, 18 ins. when extended.

Colour of proboscis is ashy-grey, passing at its base into dark green. The body is a black-green.

Longitudinal muscles continuous.

The numerous papillae are more densely packed dorsally and posteriorly than elsewhere. Anal trees, sac-like, broad and short.

LOCALITY. Trieste.

Species 19. Thalassema hupferi. Fischer.

Fischer. Abh. Ver. Hamburg, Vol. XIII. 1895, p. 20.

Described from an injured and incomplete specimen.

Length of body (?), 1.5 cm. Length of proboscis, 5 mm.

Colour, light yellow.

Papillae, small and uniformly distributed.

Longitudinal muscles, 10-11 bundles.

Nephridia, one pair, with spirally coiled internal openings.

LOCALITY. Nyango, W. Africa. On soft ground, 6 fathoms deep.

Species 20. Thalassema kokotoniense. Fischer. Plate XXXIII. Fig. 3.

Fischer. Jahrb. Hamburg. Anstalt, 1Xth year. Pt. 11. 1891, p. 82.

Described from a single specimen.

Length of body, 4·2—4·5 cm. Greatest diameter, 1·7 cm. The hinder part of the body is the broader. Proboscis absent in Fischer's specimen but present in mine, and 1·2 cm. long.

Colour, light green, rather bluish, becoming darker posteriorly.

Papillae, distributed all over the body, smaller anteriorly, arranged in more or less definite transverse rows, which are interrupted by rings of larger papillae. The larger posterior papillae are reddish.

Longitudinal muscles, 17-18 bundles.

Nephridia, three pairs, with spirally twisted internal openings.

Anal trees, with well-marked funnels.

LOCALITY. Kokotoni, E. Africa; and Blanche Bay, New Britain.

Species 21. Thalassema lankesteri. Herdman.

Herdman. Quart. J. Micr. Sci. N.S. Vol. XL, 1898, p. 381.

Described from three large fragments.

Length of body about 10 cm., the proboscis nearly as long as body.

Colour, in the living animal, apple or chrome green on the trunk, lighter on the proboscis.

The skin evenly tuberculated all over.

Longitudinal muscles, continuous.

Nephridia, one pair, with spirally twisted internal openings.

Anal trees, branched, with funnels at tips of branches.

LOCALITY. Off the Isle of Man, 50 fathoms. From a stiff blue mud bottom.

Species 22. Thalassema leptodermon. Fischer.

Fischer. Jahrb. Hamburg. Anstalt, 1xth year. Pt. II. 1891, p. 84.

Described from three mutilated specimens.

Length of body, 3.5 cm. Length of proboscis, 1.5 cm. Cylindrical body with a slight constriction round the middle.

Colour, yellow in spirit.

Papillae, distributed all over the body; they are biggest and thickest at a zone near the hinder end, and are absent at the extreme posterior end. The skin is very soft.

Longitudinal muscles, 15—16 bundles.

Nephridia, three pairs, with spirally twisted internal openings.

Anal trees, of almost uniform diameter, with numerous funnels. The rectum bears a spherical diverticulum.

LOCALITY. Zanzibar, Bueni Riff.

Species 23. Thalassema mellita. Conn.

Conn. Stud. Johns Hopkins Univ. Vol. III. 1884—1887, p. 351.

Length of body, one inch. Length of proboscis, several inches.

Colour, dull red with a light yellow proboscis, and eight white bands representing the longitudinal muscles.

Skin, nearly smooth, but minute whitish papillae round anus.

Longitudinal muscles, in 8 bundles.

Nephridia, two pairs.

LOCALITY. Found off Beaufort, living in empty Sand-dollar tests (*Mellita*, a Clypeastrid genus). The *Thalassema* enters whilst small but soon grows too large to leave its house.

Species 24. Thalassema moebii. Greef.

Greef. Acta Ac. German. Vol. XLI. Pt. II. 1879, p. 152.

Von Drasche, Verh, Ges. Wien, Vol. xxx. 1881, p. 621.

Fischer. Zool. Forschungsr. in Australien etc., Semon, Vol. v. Pt. III. 1896, p. 338.

Von Drasche thinks that this species is identical with the *Th. erythrogrammon* of Max Müller.

But Lampert very definitely states that in *Th. moebii* the longitudinal muscles are continuous and not broken up into bundles, a character in my opinion of more importance than that of the number of bundles, on which so many of the species have been practically founded.

Length of body, 7 cm. extended. Diameter of body averages about 2 cm. Length

of proboscis, 8 cm. extended.

Colour of proboscis is light green with bright yellow edges. The body is a dirty greyish-yellow, passing in some places into violet, and violet stripes run spirally round the body.

Papillae irregularly scattered over all the body, often arranged in clumps.

Longitudinal muscles, continuous.

Nephridia, three pairs, with spirally twisted openings into the body-cavity.

Anal trees, long, thin and brown, at one time stated to be without funnels, but Fischer has found them.

Sexes alike.

LOCALITY. Mauritius; Amboina; Upolu. In tubes and holes in the coral sand.

Species 25. Thalassema neptuni. Gaertner. Plate XXXIII. Figs. 4 and 5.

Greef. Acta Ac. German. Vol. XLI. Pt. II. 1879, p. 145.

Length of body, expanded 1", contracted, 5". Length of proboscis, three or four times length of body when extended.

Colour of proboscis is golden yellow, of the body orange yellow, the middle of the body is pink, and behind it is white.

Longitudinal muscles. Like Lampert I can find no mention of the condition of the longitudinal muscles in this species, in the literature of the subject, but I have satisfied myself by the dissection of some specimens from Plymouth, that these muscles form a continuous sheath and are not divided into bundles.

Nephridia, two pairs, with their internal openings spirally twisted.

LOCALITY. English Channel, South Irish Coast. In holes in the rocks, cavities in red sandstone, etc.

Species 26. Thalassema pellucidum. Fischer.

Fischer. Abh. Ver. Hamburg, Vol. XIII. 1895, p. 19.

Length of body averages 2.5 cm. Length of proboscis, 6 mm.

Colour. The young forms are light yellow, the older forms are bluish.

Papillae small and distributed over all the body, but on the pointed posterior end they are bigger and more crowded.

Longitudinal muscles, 13 in number, visible through the skin. The space between neighbouring bundles is broader than the bundles.

Nephridia, two pairs, with spirally twisted internal openings.

Anal trees about one-fourth as long as body, with single—not branched—diverticula, each ending in a funnel.

LOCALITY. Whydah, W. Africa. In mud at 5 and 5½ fathoms.

Species 27. Thalassema semoni. Fischer.

Fischer. Zool. Forschungsr. in Australien etc., Semon, Vol. v. Pt. III. 1896, p. 338.

Length of body, 5.5 cm. in larger of two specimens. The proboscis was absent. Colour of body, bluish-grey.

Papillae uniformly distributed, almost touching one another.

Longitudinal muscles in a continuous sheath.

Nephridia, two pairs, with spirally rolled internal openings.

Anal trees, thin and brown, longer than half the body-length and attached by muscles to the body-wall.

LOCALITY. Amboina.

W. III.

Species 28. Thalassema sorbillans. Lampert.

Lampert. Zeitschr. wiss. Zool. Vol. XXXIX. 1883, p. 340.

Length of body averages 4.4 cm. Length of proboscis, 2.1 cm. The body is markedly pointed both behind and in front.

Colour not mentioned.

Papillae on the posterior end. Skin thin.

Longitudinal muscles, 13 bundles.

Nephridia, three pairs, with spirally twisted inner ends. The anterior pair open in front of the ventral hooks.

Anal trees, large and brown, with funnels clearly visible under the microscope. A small diverticulum is present on the rectum.

LOCALITY. Philippines.

Species 29. Thalassema stuhlmanni. Fischer.

Fischer. Jahrb. Hamburg. Anstalt, 1xth year, Pt. 11. 1891, p. 82.

Fischer, Abh. Ver. Hamburg, Vol. XIII. 1895, p. 20.

Length of body averages 2 cm. Length of proboscis, 0.5 cm.

Colour, light gravish-brown.

Papillae, larger posteriorly where they are most closely crowded together.

Longitudinal muscles, 15—16 bundles.

Nephridia, three pairs.

Anal trees, half as long as body, with manifest funnels.

LOCALITY. Zanzibar, Bueni Riff; Pangani, Ras Muhesa.

Species 30. Thalassema vegrande. Lampert.

Lampert. Zeitschr. wiss. Zool. Vol. XXXIX. 1883, p. 341.

Shipley. P. Zool. Soc. London, 1898, p. 472.

Length of body, 3.5 cm. Greatest diameter, 1.4 cm. Proboscis absent or possibly lost, but no trace of its having existed is found.

Colour unknown.

Papillae scattered over the whole body, larger and more numerous posteriorly. Skin very thin and papery.

Longitudinal muscles, continuous.

Nephridia, three pairs. All open behind the ventral hooks. Their internal openings are spirally twisted.

Anal trees, long, brown and thin, stated to be without funnels. (?)

LOCALITY. Philippines. Rotuma.

Species 31. Thalassema viridis. Verrill.

Verrill. P. U.S. Mus. Vol. II. 1879, p. 183.

Webster. International Dictionary, under "Spoon-worm," p. 1391, Figure.

Length of body, about 6 mm. Body round, thick, about twice as long as broad, largest and obtusely rounded posteriorly. Proboscis long and slender and somewhat spoon-shaped at the end.

Colour, bright grass green in the living specimens.

The skin is "minutely granulous in appearance, the granules in circular lines."

Longitudinal muscles. Condition unknown.

Nephridia. Unknown.

LOCALITY. Off Head Harbour, Campo Bello Island, U.S.A. Found in holes in hard nodules of blue clay at 77 fathoms.

Professor Verrill has been kind enough to write to me that this species seems very rare, at all events it has been very rarely taken.

## ANALYTICAL KEY TO THE SPECIES OF THALASSEMA.

It has been found impossible to incorporate Verrill's species *Th. viridis* in the following key, as we have no knowledge of the condition of the longitudinal muscles or of the number of the nephridia.

| or or the nu                         | mber of t               | пе перии   | ura.                                 |  |                            |             |  |
|--------------------------------------|-------------------------|--|--------------------------------------|--|----------------------------|-------------|--|
| Longitudinal                         | 1 pair of<br>nephridia  | ( proboscis<br>proboscis<br>proboscis<br>proboscis | about as I small not very v wide and | ong as boc<br>wide, triloh<br>indented a | ly<br>ed at ti<br>t tip, b | ipilobed    | Th. diaphanes, Sluiter. Th. faex, Selenka. Th. giqus, Max Müller. Th. lankesteri, Herdman.   |
| muscles in a<br>continuous<br>sheath | 2 pairs of<br>nephridia | ······································             |                                      |  | • • • • • • • • • •        | *********** | Th. neptani, Gaertner. Th. semoni, Fischer.  |
|                                      | 3 pairs of<br>nephridia | with protein with no                               | boscis<br>proboscis (?               | )  |                            | •••••       | Th. mochii, Greef. Th. vegrande, Lampert.  |
|                                      | 1 pair of<br>nephridia  |  |                                      |  |                            |             | Th. hupferi, Fischer.  |
| Longitudinal muscles                 | 2 pairs of<br>nephridia | 17-19 by 8-10<br>- 7-8<br>- 8<br>  13              | undles of lo                         | ngitudinal                               | **                         |             | Th. baronii, Greef. Th. exilii, Fr. Müller. Th. formosulum, Lampert. Th. mellita, Conn. Th. pellucidum, Fischer.                   |
| divided into bundles                 | 3 pairs of<br>nephridia | 15-16  |                                      |  |                            |             | Th. caudex, Lampert. Th. erythrogrammon, Max Müller. Th. kokotoniense, Fischer. Th. leptodermon, Fischer. Th. sorbillans, Lampert. |
|                                      |                         | 15-16  | **                                   | **                                       | **                         |             | . Th. stuhlmanni, Fischer.   |

#### PART III.

#### GEOGRAPHICAL DISTRIBUTION.

The examination of the localities from which the above-mentioned species have been collected brings out certain points of interest in the geographical distribution of the genera.

The genus Bonellia reaches its northern limit in the species B. viridis, which has been found off the coast of Norway whose shores are washed by the Gulf Stream, and its southern limit at Port Jackson, Australia, where the same species occurs. It has also been found in the Mediterranean Basin and at the Loyalty Islands. B. suhmii was dredged at a great depth off the coast of Nova Scotia. B. minor is Mediterranean, and B. pamicea was found not far from Krakatoa. On the whole the genus inhabits the warm and temperate seas.

Echiurus chilensis is found in the Straits of Magellan, E. forcipatus off the coast of Greenland, E. pallasii in the North Sea, North Atlantic, and English Channel, and E. unicinctus in the Japanese waters. It is thus evident that this genus is a denizen of the colder seas and reaches from the arctic to the cooler waters of the temperate regions of both hemispheres.

Hamingia has been found 200 miles north of Cape North and again in the Hardanger fjord, and is, according to our present knowledge, an arctic and sub-arctic form.

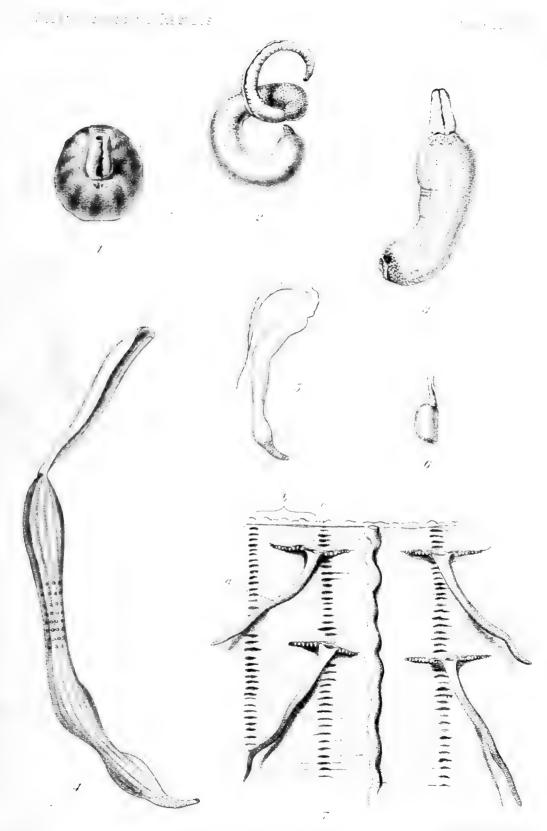
Saccosoma was found at a depth of 1215 fathoms, about half-way between Norway and Iceland, and is thus again a Northern form.

Thalassema is of all the genera of Echiuroids the most prolific in species. Of the 21 species described above only one (Th. faex) has been taken from the colder waters, and the temperature of its locality "off the coast of Norway" is much mitigated by the Gulf Stream. Th. lankesteri was found off the Isle of Man, Th. neptuni in the English Channel, and Th. gigas at Trieste. The remaining sixteen species are all from tropical or sub-tropical seas. Five of these occur in the Atlantic, and eleven have been found in the Indian Ocean, the Red Sea and the South-West area of the Pacific. The genus is thus more markedly a lover of the warm water than is Bonellia. The remaining three genera taking their place in the colder temperate or arctic seas of both hemispheres.

The Zoological Laboratory, Cambridge,  $February, \ 1899.$ 

#### EXPLANATION OF PLATE XXXIII.

- Fig. 1. An anterior and slightly ventral view of Thalassema baronii. Natural size.
- Fig. 2. A view of Thalassema diaphanes.  $\times 1.5$ .
- Fig. 3. A ventral view of Thalassema kokotoniense. Natural size.
- Fig. 4. A sketch of *Thalassema erythrogrammon* taken from a drawing made by Dr Willey from the living specimen. The papillae, which are much more apparent when the animal is in a state of contraction, are only shown over a small band, but they are not confined to this band.
  - Fig. 5. A view of Thalassema neptuni, killed in an expanded condition.
- Fig. 6. A view of *Thalassema neptuni*, killed in a contracted condition. The specimens in figures 5 and 6 weigh almost exactly the same, they are drawn so as to show the differences of size and outline produced by the method of killing.
- Fig. 7. A portion of the skin of a *Thalassema baronii* taken from the ventral surface, showing the nervous system, the coiled internal openings of the four nephridia a, the longitudinal muscles b, and the intervals between adjacent muscles c.



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